Spatiotemporal variations in the growth status of declining wild apple trees in a narrow valley in the western Tianshan Mountains, China

QIU Dong[1,2], TAO Ye[2], ZHOU Xiaobing[2], Bagila MAISUPOVA[3], YAN Jingming[2], LIU Huiliang[2], LI Wenjun[2], ZHUANG Weiwei[1*], ZHANG Yuanming[2*]

[1] Xinjiang Key Laboratory of Special Species Conservation and Regulatory Biology/Key Laboratory of Special Environment Biodiversity Application and Regulation in Xinjiang/Key Laboratory of Plant Stress Biology in Arid Land/College of Life Sciences, Xinjiang Normal University, Urumqi 830054, China;

[2] State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China;

[3] Kazakh Scientific Research Institute of Forestry and Agroforestry, Astana 010000, Kazakhstan

Abstract: *Malus sieversii* (wild apple tree), only distributed in the Tianshan Mountains in Central Asia, is a tertiary relic species and an ancestral species of cultivated apples. However, existing natural populations of wild apple trees have been declining. To date, spatiotemporal variations in the growth status of declining wild apple trees and influencing factors in the narrow valley areas in the Tianshan Mountains remain unclear. In this study, field investigation and sampling were carried out in three years (2016–2018) at four elevations (1300, 1400, 1500, and 1600 m) in the Qiaolakesai Valley (a typical longitudinal narrow valley in the Yili River Valley) of the western Tianshan Mountains in Xinyuan County, Xinjiang Uygur Autonomous Region, China. Projective coverage, dead branch percentage, and 18 twig traits (these 20 parameters were collectively referred to as plant traits) were determined to comprehensively reflect the growth status of declining wild apple trees. The values of dead branch percentage ranged from 36% to 59%, with a mean of 40%. Year generally showed higher impact on plant traits than elevation. In 2017 and 2018, projective coverage, leaf size, leaf nitrogen concentration, and nitrogen to phosphorous ratio were markedly higher than those in 2016. However, dead branch percentage and leaf and stem phosphorous concentrations showed the opposite trend. Most of the topological parameters of plant trait networks differed in the three years, but the strength of trait–trait association increased year by year. The mean difference between day and night temperatures (MDT), annual accumulative precipitation, soil electrical conductivity, and soil pH had the greatest impact on the plant trait matrix. The growth status of declining wild apple trees was directly and positively affected by MDT and leaf size. In conclusion, the growth of declining wild apple trees distributed in the narrow valley areas was more sensitive to interannual environmental changes than elevation changes. The results are of great significance for further revealing the decline mechanism of wild apple trees in the Tianshan Mountains.

Keywords: *Malus sieversii*; plant attributes; plant trait network; elevation gradient; meteorological factor; western Tianshan Mountains

Citation: QIU Dong, TAO Ye, ZHOU Xiaobing, Bagila MAISUPOVA, YAN Jingming, LIU Huiliang, LI Wenjun, ZHUANG Weiwei, ZHANG Yuanming. 2022. Spatiotemporal variations in the growth status of declining wild apple trees in a narrow valley in the western Tianshan Mountains, China. Journal of Arid Land, 14(12): 1413–1439. https://doi.org/10.1007/s40333-022-0087-8

*Corresponding authors: ZHUANG Weiwei (E-mail: zww8611@sina.com); ZHANG Yuanming (E-mail: ymzhang@ms.xjb.ac.cn)
The first and second authors contributed equally to this work.

Received 2022-03-14; revised 2022-10-14; accepted 2022-10-21

1 Introduction

Malus sieversii (wild apple tree) is a tertiary relict species. It is also a rare plant species under second-class national protection in China and is categorized as Vulnerable on the IUCN Red List (Zhang, 1973; Zhang et al., 2015, 2021; Cui et al., 2019). Wild apple trees are discontinuously distributed in the Yili River Valley of the western Tianshan Mountains in China, Kazakhstan, and Kyrgyzstan (Zhang et al., 2019). Owing to the special geographical location and climatic conditions (i.e., marine climate and inversion layer), the Tianshan Mountains have become the last refuge for many deciduous broad-leaved wild fruit tree species in Central Asia (Zhang et al., 2015). In the process of geological and historical changes, *M. sieversii* has experienced long-term natural selection and evolution and has become a key material to reveal the paleoclimate change and the evolution of species distribution pattern in the Tianshan Mountains (Zhang et al., 2015, 2021). *M. sieversii* is a valuable germplasm resource with many different stress resistance characteristics. At least 84 infra-species of *M. sieversii* have been identified in the Yili River Valley alone (Yan and Xu, 2010). Recent studies have demonstrated that *M. sieversii* distributed in the Yili River Valley is an ancestral species of cultivated apples (Duan et al., 2017; Wang et al., 2018; Spengler, 2019). Thus, it is of great value to the conservation of the precious germplasm resources (Chen et al., 2021; Liao et al., 2021). However, in recent decades, the survival of wild apple trees has been strongly disturbed by diseases, insect pests (mainly *Agrilus mali*), grazing, human deforestation, and climate change (Cui et al., 2019; Zhang et al., 2021). Therefore, a large number of wild apple trees have withered and died. In addition, the natural seedling renewal rate of wild apple tree is extremely low, and the populations are facing the risk of severe degradation or even extinction (Su et al., 2019; Tao et al., 2020; Zhang et al., 2020; Yan et al., 2022). As such, understanding the physiological and ecological processes of wild apple trees related to the decline is of great significance to the ecological conservation and sustainable utilization of the precious germplasm resources.

Plant growth performance is a comprehensive reflection of multiple organs and functions (Liu and Ma, 2015; Falster et al., 2018). The appearance of aboveground parts of woody plants is closely related to their branches. The twigs of woody plants (composed of the supporting components of the current-year stem and the photosynthetic components of leaves; hereinafter referred to as stems and leaves) are among the most active components of plants (Westoby and Wright, 2003; Yao et al., 2015; Li et al., 2017). Leaves are the main photosynthetic organs of plants, whereas stems support the leaves and play a crucial role in the transportation and storage of products by photosynthesis and in the conduction of water and minerals (Niinements et al., 2006; Lambers, 2008). The functioning of twigs is related to various traits. Twig traits can be comprehensively characterized by multiple indicators, such as morphological or structural (e.g., leaf size, specific leaf area, and biomass allocation), physiological (e.g., photosynthesis, respiration, and enzyme activity), and chemical (e.g., element and compound contents) indicators, which are the integrative reflection of plant growth response and environmental adaptation (Yang et al., 2010; Liu and Ma, 2015; Li et al., 2017). The trade-offs between stem and leaf traits and among different functional traits are the results of plants' adaptation to environmental heterogeneity (He et al., 2018; He et al., 2019; Zhang et al., 2021). For instance, leaves usually have higher nutrient content than stems to support their high physiological activity (He et al., 2019; Luo et al., 2021). Plants adapt to environmental changes by regulating and changing some of their functional traits and form different survival strategies (Liu and Ma, 2015; Zhang et al., 2021). Therefore, the introduction of more traits and the identification of key traits can accurately reflect the comprehensive response and adaptation of plants to environmental changes and are conducive to the in-depth disclosure of plant survival strategies (He et al., 2020).

Elevation is an important factor causing variation in plant traits and change in plant adaptation. It is a comprehensive environmental factor that affects the growth and physiology of plants through changes in micro-terrain, light, temperature, soil, vegetation, and other factors (Fang et al., 2004; Song et al., 2011; Gong et al., 2020). With increasing elevation, light intensity and the

consumption of plant protease increase gradually, and thus the content of nitrogen (N) in plant leaves decreases. However, low temperatures caused by increasing elevation can increase the content of protective enzymes, and the accumulation rate of leaf N is higher than the consumption rate of leaf N, actually resulting in the increasing of leaf N content with increasing elevation (Lambers, 2008; van de Weg et al., 2009; Song et al., 2011). Thus, as elevation increases, a trade-off between temperature and sunshine occurs (Wang and Wang, 2015). Soil variables are correlated to plant nutrients at different elevations, but the interpretation of soils to variations in plant physiological traits is usually lower than that of temperature and precipitation (Gong et al., 2020). In addition to elevation, plant traits in natural ecosystems usually exhibit obvious interannual variation, which is mainly related to the interannual fluctuation of climate (e.g., precipitation, air temperature, and sunshine hours (Pérez-Camacho et al., 2012; Du et al., 2021; Richmond et al., 2021), and different plant species and various plant traits are likely to present differential interannual variation patterns (Mendes et al., 2014). Climatic characteristics and vegetation composition generally differ among regions, so the elevational and interannual variation patterns of plant traits are inconsistent to a large extent, and the influencing factors are complex and diverse.

By contrast, the rate of decline in wild apple trees distributed in the valley areas is relatively lower than that along the mountains (Yan et al., 2022). Significant differences in the genetic diversity of *M. sieversii* have been found among different elevations in the valley areas, and a unimodal distribution pattern has been observed. Wild apple trees distributed at low, medium, and high elevations show significant genetic differentiation, indicating that elevation exerts an important impact on the genetic diversity and genetic structure of wild apple populations (Zhang and Zheng, 2020). However, little is known about whether notable differences exist in the growth status of declining wild apple trees at different elevations in the narrow valley areas and whether interannual changes in their growth status occur. Moreover, in the context of global or regional climate change (Chen et al., 2011; Li et al., 2021), the key driving forces of growth change in declining wild apple trees in the Tianshan Mountains remain unclear.

In this study, adult wild apple trees in natural populations at four elevations (1300–1600 m, at an interval of 100 m) in the Qiaolakesai Valley (a typical longitudinal narrow valley in the Yili River Valley) of the western Tianshan Mountains in Xinyuan County, Xinjiang Uygur Autonomous Region, China were selected as the research object to analyze the growth status of declining wild apple trees during 2016–2018, and the analyzed parameters included the projective coverage (PC), dead branch percentage (DBP), and a series of twig traits. The objectives were as follows: (1) to explore the spatiotemporal variation characteristics of plant traits; (2) to reveal twig trait associations; and (3) to clarify the relationships between plant traits and environmental factors. The results will help to reveal the decline mechanism of wild apple trees and provide a theoretical basis for the scientific management of the precious germplasm resources in the Tianshan Mountains in Central Asia.

2 Materials and methods

2.1 Study area

The Tianshan Mountains are a large mountain range in Central Asia and stretch about 2500.0 km. They are also the largest mountain chain in the world's temperate arid region and the largest isolated east–west mountain range globally. The Tianshan Mountains have the richest biodiversity in Central Asia, especially the Yili River Valley. This area is rich in water resources, and there are small valleys with different directions or widths (Hu, 2004; Xiong, 2017). Wild apple trees are usually distributed on the northern slope of the Tianshan Mountains at elevations of 1000–1700 m (Yan and Xu, 2010).

The bottom of the study area (the Qiaolakesai Valley in the Yili River Valley of the western Tianshan Mountains in Xinyuan County, Xinjiang Uygur Autonomous Region, China;

43°22′48″N, 83°25′13″E; Fig. 1) has a stream, with the width of approximately 3.0 m and the slope of 25°–35°. More than 50.0 m away from the stream, there are wild apple trees growing on its east and west sides. The climate in the study area (the Qiaolakesai Valley) is temperate continental, with wet spring and summer and snowfall in winter (Zhang 1973; Yan and Xu, 2010). An "inversion layer" region exists between 800 and 1600 m elevations in the Yili River Valley. The temperature in this region increases with increasing elevation or remains relatively stable (Yan and Xu, 2010). In Xinyuan County, the temperature in the plain region can be as low as –10 ℃ in January, while the average temperature in the inversion layer region is only about –3 ℃. The annual precipitation in the inversion layer region (up to 400–500 mm) is higher than that in the plain region (320–400 mm) (Yan and Xu, 2010). The inversion layer is an important reason for the high plant diversity and productivity in this region. Meanwhile, the distribution range of wild apple trees is just in the inversion layer region.

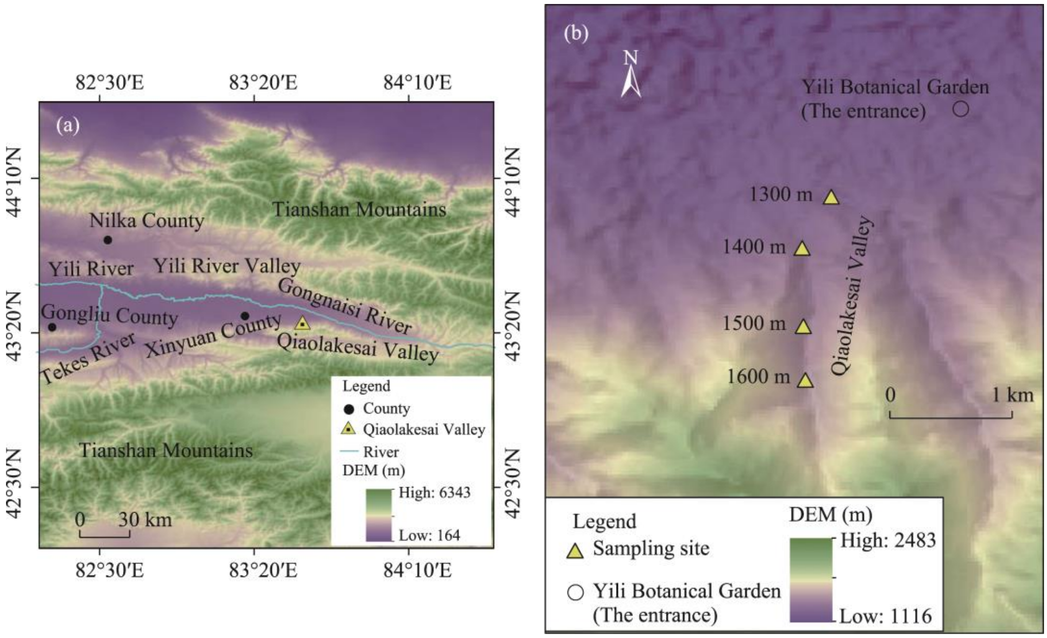

Fig. 1 Location of the study area (the Qiaolakesai Valley) in the Yili River Valley of the western Tianshan Mountains in Xinyuan County, Xinjiang Uygur Autonomous Region, China (a) and the distribution of sampling sites of declining wild apple trees at four elevations in the Qiaolakesai Valley (near the Yili Botanical Garden) (b). Note that no wild apple trees are distributed at elevations lower than 1300 m and higher than 1600 m. DEM, digital elevation model.

In Xinyuan County, wild apple trees generally exist as pure forest. Two main distribution patterns have been observed (Yan and Xu, 2010). The first pattern is that wild apple trees are horizontally distributed along the mountain, and the elevation range is relatively narrow (mainly 1300–1500 m), but the density and canopy density of wild apple trees are relatively high. The second pattern is that trees are scattered in the longitudinal valleys with different widths. Although the elevation range is slightly large in these longitudinal valleys, the population size is relatively small, and the density and canopy density of wild apple trees are relatively low (Yan and Xu, 2010; Xiong, 2017; Zhang and Zheng, 2020).

2.2 Experimental design and twig sampling

According to the upper and lower limits of the actual distribution of declining wild apple trees in the Qiaolakesai Valley, we finally identified four sampling sites at four elevations (1300, 1400, 1500, and 1600 m; Fig. 1), and set up two repeated sampling plots on both east and west sides of the valley in each sampling site (Yan et al., 2021). The plot size was designed as 30 m×30 m (an

area of 900 m^2). Six moderate-sized declining wild apple trees were selected for labeling and sampling in each plot. Thus, each elevation (sampling site) sampled 12 trees, and 48 trees were included in an annual field survey. The density of declining wild apple trees at each elevation ranged from 8 to 12 individuals per sampling plot (i.e., 900 m^2), and no significant differences in plant height and basal diameter of the selected trees were determined, although they tended to decrease with increasing elevation (Fig. S1). Field survey sampling was carried out in later July for three consecutive years (2016–2018).

During field survey sampling, for each wild apple tree, two twig samples were collected using a high branch scissors in each of the four directions in the middle part of the tree canopy, and then eight twig samples were obtained. Three to four fresh and intact leaves were extracted from the middle to the upper part of each twig, and 30 leaves and eight stems per tree were collected and considered one sample. The stem and leaf samples were immediately placed in envelopes and stored in a foam incubator with ice bags (Yan et al., 2022). The coordinates, elevations, and topographical parameters of the sampling plots were recorded using a GPS (GPSMAP®60CSx, Garmin, Orasi, USA) during the first survey.

2.3 Determination of twig traits

All plant samples were taken back to the laboratory of the Yili Botanical Garden, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, China. The leaves were scanned with a scanner (CanoScan LIDE120, Canon, Tokyo, Japan) at 600 dpi and analyzed by a Plant Image Analyzer (LA-S, Wanshen Testing Technology Co. Ltd., Hangzhou, China) to determine the individual leaf area (LA). We calculated the LA based on all leaf areas and leaf number sampled in one tree. The leaf and stem samples were oven-dried at 70 ℃ to constant weight and then weighed (accurate to 0.1 mg). The individual leaf weight (LW) was determined using all the leaf mass and leaf number sampled in one tree, and the leaf mass per unit area (LMA; LMA=LW/LA) was further calculated.

Dried plant samples were milled into powder in a vibratory disc mill (RS200, Retsch GmbH Inc., Haan, Germany) and stored in zip bags. The leaf total N (mg/g), total phosphorous (P; mg/g), and total potassium (K; mg/g) concentrations were measured using an elemental analyzer (Multi N/C 3100, Analytik Jena AG, Jena, Germany), the molybdenum–antimony antispectrophotometric method, and a flame spectrophotometry (FP640, Jingke Co., Shanghai, China), respectively.

Nutrient concentrations in the stems (i.e., N_{stem}, P_{stem}, and K_{stem}) and leaves (i.e., N_{mass}, P_{mass}, and K_{mass}) were mass based (mg/g); here, we converted leaf nutrient concentrations into area-based N_{area} (mg/cm^2), P_{area} (mg/cm^2), and K_{area} (mg/cm^2) concentrations according to the LA and LW for each tree, for instance, $N_{area}=N_{mass}\times LW/LA$. Nutrient traits based on unit mass and LA are essential trait indicators reflecting plant growth and functioning (Liu and Ma, 2015; Li et al., 2022). Stoichiometric ratios (i.e., N:P, N:K, and P:K) are the same in mass-based and area-based nutrient concentrations in leaves. Therefore, twig traits were composed of leaf-related traits (12 parameters) and stem-related traits (six parameters).

2.4 Evaluation on dead branch percentage (DBP) and projective coverage (PC)

The basal diameter of the trunk (which is at 10 cm height above the trunk base and is converted by the base perimeter) and plant height were determined using a tape measure and a height rod, respectively. The DBP (%) and PC (%) of declining wild apple trees were assessed. The DBP was the percentage of dead branches per plant to the total number of branches per plant; the proportion of living branches decreases with increasing number of branches (Wang et al., 2021). The PC was the canopy area percentage of a plant (which was obtained by the following equation: crown length×width×π, where crown length and width were measured by tape measure) excluding voids, and voids were obtained using visual method (Tao et al., 2020; Yan et al., 2022).

The growth status of declining wild apple trees was comprehensively characterized by PC, DBP, and twig traits. All these 20 parameters were collectively referred to as plant traits.

2.5 Soil sampling and sample analyses

According to the distribution of declining wild apple trees in each sampling plot, we collected three replications of soil sample during each filed survey. Two nearest trees were regarded as a sampling unit, and a mixed soil sample at a depth of 0–10 cm was collected. The soil sampling points were located 1.0 m outside the trunk in four directions of declining wild apple trees. Six mixed soil samples were collected from each elevation (sampling site) in each year, and a total of 24 soil samples were taken annually for the four elevations. Soils were air-dried in the laboratory and then sieved. The concentrations of soil organic carbon (SOC; g/kg), total nitrogen (TN; g/kg), total phosphorus (TP; g/kg), total potassium (TK; g/kg), available nitrogen (AN; mg/kg), available phosphorus (AP; mg/kg), available potassium (AK; mg/kg), soil pH, and electrical conductivity (EC; μS/cm) were determined in accordance with standard methods (Bao, 2000).

2.6 Meteorological data collection

The daily temperature and precipitation data in the surveyed years were obtained from an automatic weather station (WatchDog, 2900ET, Chicago, USA) in the long-term monitoring plot in the Yili Botanical Garden, which is approximately 500.0 m away from the east of the sampling site at 1300 m elevation (Tao et al., 2020). The annual accumulative precipitation (AAP; mm), mean annual temperature (MAT; ℃), and annual mean difference between day and night temperatures (MDT; ℃) were calculated to determine their relationships with the plant traits of declining wild apple trees. The four sampling sites are located in the same valley. Although the elevation difference reaches 300 m, the horizontal straight-line distance between the sampling site at 1300 m and the sampling site at 1600 m is only 1.5 km (Fig. 1). Given that an inversion layer exists here, such elevation difference will not cause great fluctuations in temperature and precipitation. Therefore, the four sampling sites shared the same meteorological data in the same year.

2.7 Statistical analysis

All data were checked for normality using Kolmogorov-Smirnov test, and these data followed normal or log-normal distributions. Descriptive statistical analyses on plant traits were conducted, and the mean value and coefficient of variation (<25%: weak variation; 25%–75%: moderate variation; and >75%: strong variation) were obtained (Zar, 2009). Although the plant height and basal diameter of declining wild apple trees tended to decrease with increasing elevation, no significant differences of these parameters were observed among the four elevations (Fig. S1). This result indicated that the tree size effect can be neglected in subsequent statistical analyses (i.e., plant height and basal diameter were not used as random factors). Repeated measures ANOVA was used in assessing the primary and interactive effects of time (i.e., year) versus elevation; and year, elevation, and their interaction were used as factors (Zar, 2009). One-way ANOVA was used to compare plant traits in different years and at different elevations, and Tukey's HSD post hoc test was applied to compare the difference of means (α=0.05). IBM-SPSS 21.0 (SPSS Inc., Chicago, Illinois, USA) was used for data analyses. The data were presented as mean±standard error (SE).

In this study, we used plant trait networks (PTNs) to explore the relationships among a series of twig traits in different years or elevations (Kleyer et al., 2019; He et al., 2020; Li et al., 2021). The matrix of trait–trait relationships was calculated, and the correlation coefficient (r) was quantified using Spearman's method and the "psych" package in R 4.0.5 (https://www.r-project.org/). To remove spurious correlations among traits, we set up the threshold of adjacency matrix at the P<0.05 level. Finally, the PTN and its topological parameters were visualized using the "igraph" package in R 4.0.5 (Kleyer et al., 2019; Rao et al., 2022). In the PTN, a trait is considered to have the highest degree when most edges that linked this focus node trait to other nodes can be considered as a general hub trait (He et al., 2020; Li et al., 2021). High modularity can indicate relatively strong functional decoupling among traits. Low modularity means relatively high functional coupling, that is, relatively robust associations among functional traits

are present (Flores-Moreno et al., 2019; Rao et al., 2022). This statistical analysis was carried out using R 4.0.5 (https://www.r-project.org/).

To explore the relationships between plant traits and environmental factors, especially meteorological factors, we used the pooled data of all elevations and years. The Pearson's correlation analysis was used to explore the relationships between plant traits and environmental factors (including elevation, meteorological factors, and soil physical-chemical variables). Non-metric multidimensional scaling analysis was conducted to deeply explore the comprehensive influence of environmental factors on plant trait matrix based on Sørenson (Bray–Curtis) distance using PC-ORD version 5 (McCune and Mefford, 2011). Random starting configurations and 50 runs with real data and randomized data were used to compute the ordination solution, and the dimensionality of each data set was assessed by requesting a step down from a six-dimensional ordination. A stable two-dimensional solution was finally identified for the ordination. Pearson's correlation coefficients were calculated to further elucidate correlations between plant trait matrix and environmental factors in the non-metric multidimensional scaling ordination (Zar, 2009). The graph of plant traits in ordination space with overlays of environmental factors was used to describe ordination gradients.

Structural equation modeling (SEM) was used to evaluate and quantify the effects of elevation, meteorological factors, and soil physical-chemical variables on plant traits (Kline, 2010). As the individual growth status is the comprehensive embodiment of traits and functions of different plant organs, the intuitional plant growth vigor (PC and DBP) was considered as the result variable; meteorological factors were regarded as the exogenous variables; and soil EC and nutrients, twig nutrients, and leaf size (representing photosynthetic capacity) were considered as the intermediate observation variables. These variables were used to reveal the influence path and intensity of abiotic factors on plant traits (Han et al., 2011; Luo et al., 2021). Prior to SEM, we comprehensively determined the final variables used in SEM according to the method of Zhang et al. (2021). After screening the environmental factor data and plant trait data, we selected MDT, EC, and PC to represent meteorological factor, soil environment, and plant growth performance, respectively. The LA was used to reflect photosynthetic capacity. The parameters that had no significant correlations or were highly collinear were removed. And then, soil TN, TP, AN, and AK were retained to characterize the observed variable "soil nutrient". Similarly, P_{mass}, P_{area}, and P_{stem} were extracted to reflect the observed variable "twig trait". Soil nutrient and twig trait were represented by the standardized value of those selected variables (the minimum–maximum normalized average value), i.e., multiple functionality, which is a comprehensive reflection of soil nutrients or plant nutrients. We tested the fit of SEM by using the χ^2 goodness of fit test and the root mean square error of approximation (RMSEA) test. Then, we extracted the unique moments of the model, such as path coefficients and undirected correlations (Kline, 2010). The SEM analysis was performed using the "igraph" package in R 4.0.5 (https://www.r-project.org/).

3 Results

3.1 Variations in PC and DBP

All plant traits presented moderate and weak variations. The coefficients of variation of PC and DBP were the largest, while the coefficients of variation of P_{mass} and P_{stem} were the smallest (Table S1). Both PC and DBP were significantly (P<0.05) affected by year and elevation, whereas year presented higher impact on PC and DBP than elevation (Fig. 2). PC at the highest elevation (1600 m) was the lowest in 2017, whereas PC at 1400 and 1600 m showed significantly (P<0.05) higher values than that at 1300 and 1500 m in 2018. The pooled three-year data for each elevation indicated that at the highest elevation PC was the lowest but DBP was the highest (Fig. S2). At each elevation, PC presented significant (P<0.05) differences among the three years, and PC values in 2017 and 2018 were markedly higher than that in 2016. The change trend of DBP was basically opposite to that of PC, indicating that the overall growth of declining wild apple

trees was improving. This finding was confirmed by the result of the pooled four-elevational data among the three years (Fig. S3). The values of DBP ranged from 36% to 59% during 2016–2018 (with a mean of 40%), implying that the natural populations of declining wild apple trees in this region are still facing obvious declining pressure.

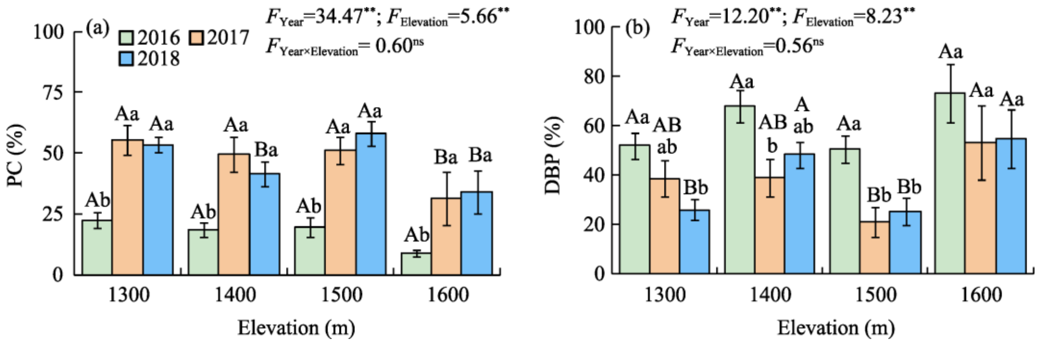

Fig. 2 Differences in projective coverage (PC; a) and dead branch percentage (DBP; b) of declining wild apple trees at different elevations in different years in the Qiaolakesai Valley. Different capital and lowercase letters indicate significant differences (P<0.05) among the four elevations in the same year and among the three years at the same elevation, respectively. A summary of the results of a repeated measures ANOVA (F value) addressing the effects of year and elevation is shown in the upper part of each panel. ** indicates that F value is significant at P<0.01 level; ^{ns} means no significance (P>0.05).

3.2 Changes in leaf traits

Results indicated that LMA and K_{area} were neither affected by elevation nor year, and no interaction existed between elevation and year (Table 1). P_{mass}, P_{area}, and LW showed significant (P<0.05) differences only between years and they were not affected by elevation and elevation–year interaction. The value of K_{mass} was only affected by elevation. The values of P:K and LA were affected by both elevation and year, but not by elevation–year interaction. Significant (P<0.05) interannual difference in N_{area} was tested, and it was also affected by elevation–year interaction. The values of N_{mass}, N:P, and N:K were significantly (P<0.05) affected by year, elevation, and their interaction.

Table 1 Summary of repeated measures ANOVA (F value) on twig traits of declining wild apple trees at different elevations in different years in the Qiaolakesai Valley

Factor	LA	LW	LMA	N_{mass}	P_{mass}	K_{mass}	N_{area}	P_{area}	K_{area}
Elevation	4.51**	0.92	0.52	10.23***	1.86	4.72**	2.18	0.37	2.52
Year	22.90***	13.46***	2.16	4.45*	21.86***	0.10	6.38**	17.31***	0.55
Elevation ×Year	0.97	0.79	0.31	21.05***	0.40	0.62	4.97***	0.72	0.80
Factor	N:P	N:K	P:K	N_{stem}	P_{stem}	K_{stem}	N_{stem}:P_{stem}	N_{stem}:K_{stem}	P_{stem}:K_{stem}
Elevation	9.15***	6.48***	4.31**	2.60	0.73	0.32	3.74**	1.15	0.49
Year	13.45***	4.08*	10.22***	3.90*	29.85***	10.98***	6.88**	5.64**	0.70
Elevation ×Year	23.64***	5.23***	0.74	7.12***	2.01	0.74	4.86***	5.75***	1.87

Note: LA, individual leaf area; LW, individual leaf weight; LMA, leaf mass per unit area; N, nitrogen; P, phosphorus; K, potassium. N_{mass}, P_{mass}, and K_{mass} indicate leaf N, P, and K concentrations per unit mass, respectively. N_{area}, P_{area}, and K_{area} indicate leaf N, P, and K concentrations per unit area, respectively. N_{stem}, P_{stem}, and K_{stem} indicate stem N, P, and K concentrations per unit mass, respectively. *, P<0.05 level; **, P<0.01 level; ***, P<0.001 level.

At different elevations, LA was the lowest at 1600 m in 2016, and no significant difference of LA was found among the four elevations in 2017. LA at 1500 m elevation was significantly (P<0.05) higher than that at 1400 and 1600 m in 2018. By contrast, LW did not present significant difference among elevations, indicating an independence of elevation (Fig. 3). According to the pooled three-year data, LA at the highest elevation (1600 m) was the lowest, whereas LW did not

show elevational difference among the four elevations (Fig. S2). At each elevation, LA values in 2017 and 2018 were significantly (P<0.05) higher than that in 2016 (except that at 1400 m in 2018), while LW gradually increased with year, although no significant difference was found at 1400 m (Fig. 3). By analyzing the pooled data of four elevations every year, we found that LA and LW were the lowest in 2016 (Fig. S3). The values of LMA kept relatively stable among different elevations and years.

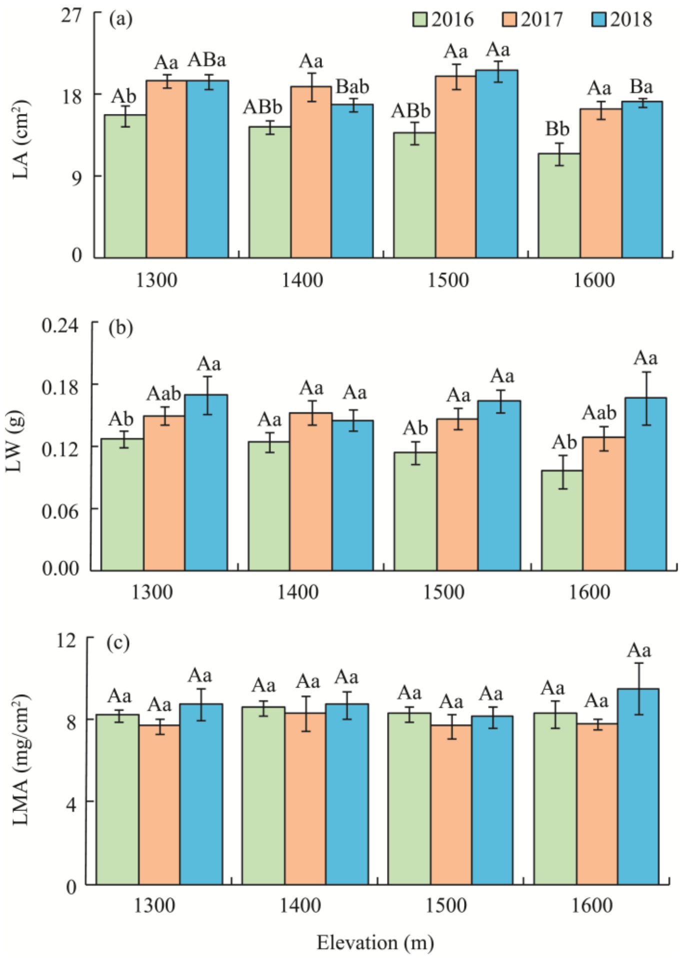

Fig. 3 Differences in individual leaf area (LA; a), individual leaf weight (LW; b), and leaf mass per area (LMA; c) of declining wild apple trees at different elevations in different years in a typical valley in the Qiaolakesai Valley. Different capital and lowercase letters indicate significant differences (P<0.05) among the four elevations in the same year and among the three years at the same elevation, respectively.

N_{mass} and N_{area} presented obviously interannual differences among different elevations. N_{mass} and N_{area} increased with increasing elevation in 2016 and 2018 but the values showed the opposite trend in 2017 (Fig. 4). The ANOVA among the four elevations for the pooled three-year data showed no elevational difference for both N_{mass} and N_{area} (Fig. S4). In 2016, P_{mass} increased with increasing elevation, but no significant changes were found in 2017 and 2018. P_{area} did not show significant change with increasing elevation. In 2018, K_{mass} was the highest at 1500 m, and K_{area} was the highest at 1400 m in 2017 (Fig. 4). Except these two cases, K_{mass} and K_{area} represented no significant difference among different years or elevations. As shown in Figure S4, P_{mass}, P_{area}, and K_{area} did not exhibit obvious elevational difference, but K_{mass} showed the highest value at 1500 m and the lowest value at 1600 m. At each elevation, the mass- and area-based leaf N and P concentrations generally showed significant (P<0.05) but inconsistent interannual differences (Fig. 4). This result was confirmed in the comparative analysis of the pooled four-elevation data

among the three years (Fig. S5). That is, N_{mass} and N_{area} were the lowest in 2016 and the highest in 2018, and P_{mass} and P_{area} in the three surveyed years showed a pattern of 2016>2018>2017.

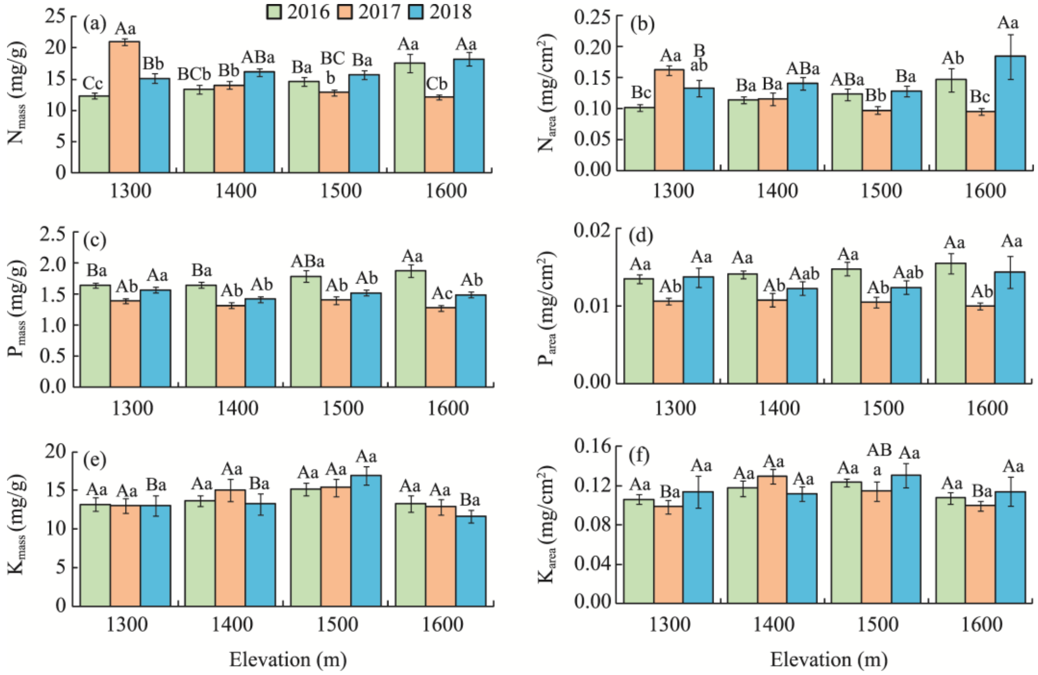

Fig. 4 Differences in leaf nutrient concentrations per unit mass (a, c, e) and leaf nutrient concentrations per unit area (b, d, f) of declining wild apple trees at different elevations in different years in the Qiaolakesai Valley. N, nitrogen; P, phosphorus; K, potassium. N_{mass}, P_{mass}, and K_{mass} indicate leaf N, P, and K concentrations per unit mass, respectively. N_{area}, P_{area}, and K_{area} indicate leaf N, P, and K concentrations per unit area, respectively. Different capital and lowercase letters indicate significant differences (P<0.05) among the four elevations in the same year and among the three years at the same elevation, respectively.

In 2017, leaf N:P was the highest at 1300 m, and no significant difference of leaf N:P among the other three elevations was found. In 2016, leaf N:P was the highest at 1600 m and the lowest at 1300 m, and no elevational difference of leaf N:P was found in 2018 (Fig. 5). According to the ANOVA result for the pooled three-year data among the four elevations, leaf N:P showed no significant elevational difference among the four elevations (Fig. S4). Except for the 1300 m elevation, leaf N:P increased year by year at the other three elevations, indicating that N limit was gradually alleviated. This finding was confirmed in the comparative analysis of the pooled four-elevation data among the three years (Fig. S5). Leaf N:K and P:K showed elevational and interannual differences to an extent (Figs. S4 and S5).

3.3 Changes in current-year stem traits

P_{stem}:K_{stem} was neither affected by elevation nor year, and no interaction existed between elevation and year (Table 1). P_{stem} and K_{stem} showed significant (P<0.05) differences only between years. Significant (P<0.05) interannual differences in N_{stem} and N_{stem}:K_{stem} were tested, which were also affected by the elevation–year interaction. N_{stem}:P_{stem} not only presented significant (P<0.05) differences between years or elevations but also was affected by their interaction.

Except for P_{stem}:K_{stem}, all stem traits were mainly affected by year, and elevation only showed a significant (P<0.05) effect on N_{stem}:P_{stem} (Table 1). With increasing elevation, N_{stem} gradually decreased in 2016 and increased in 2017, but increased first and then decreased in 2018 (Table S2). Except for P_{stem} at 1500 m in 2017 (which showed the highest value), P_{stem} and K_{stem} did not exhibit elevational differences in each year. In 2017 and 2018, P_{stem} was generally low, but K_{stem}

was relatively low in 2017. N_{stem}:P_{stem} presented completely different change trends with increasing elevation among the three years. The change trend of N_{stem}:K_{stem} was basically the same as that of N_{stem}:P_{stem}. The regularity of P_{stem}:K_{stem} did not obviously change with increasing elevation, and no significant elevational difference of P_{stem}:K_{stem} was found among the three years at all elevations, with an exception of 1300 m.

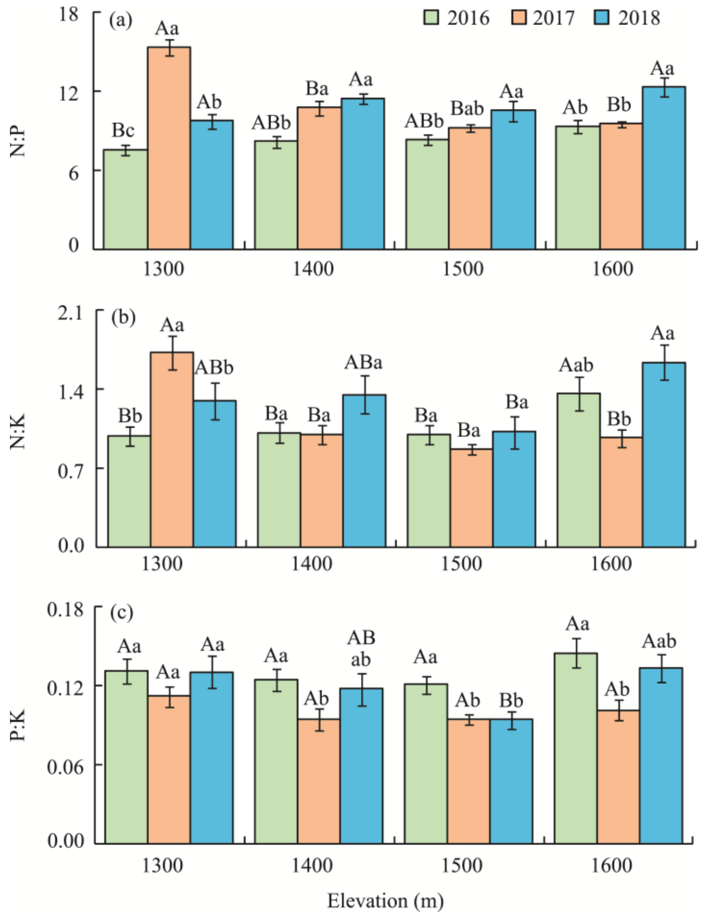

Fig. 5 Differences in leaf N:P (a), N:K (b), and P:K (c) of declining wild apple trees at different elevations in different years in the Qiaolakesai Valley. Different capital and lowercase letters indicate significant differences (P<0.05) among the four elevations in the same year and among the three years at the same elevation, respectively.

3.4 Associations among twig traits in different years

Overall, year presented higher impact on twig traits than elevation, so three PTNs were used to correspond to the pooled four-elevation data for the three years. The PTN edge number in 2016 (43) was lower than that in 2017 (50) and 2018 (47), as well as the average degree, centralization betweenness, centralization degree, and connectance (Table S3). The modularity index value of PTN in 2016 was higher than those in 2017 and 2018, indicating a low degree of functional decoupling (i.e., high functional coupling) in 2017 and 2018. The hub traits that had the highest degree differed among the three years, while all of them belonged to leaf nutrient traits (Fig. 6; Table S4). In addition, the traits with the highest betweenness differed among years, indicating that the strongest mediating effects in the PTNs were expressed by different twig traits in different years. In any case, the healthier the growth status is, the closer the twig trait association is. Consequently, network associations among twig traits changed obviously in different years, and this change might be related to interannual environmental change.

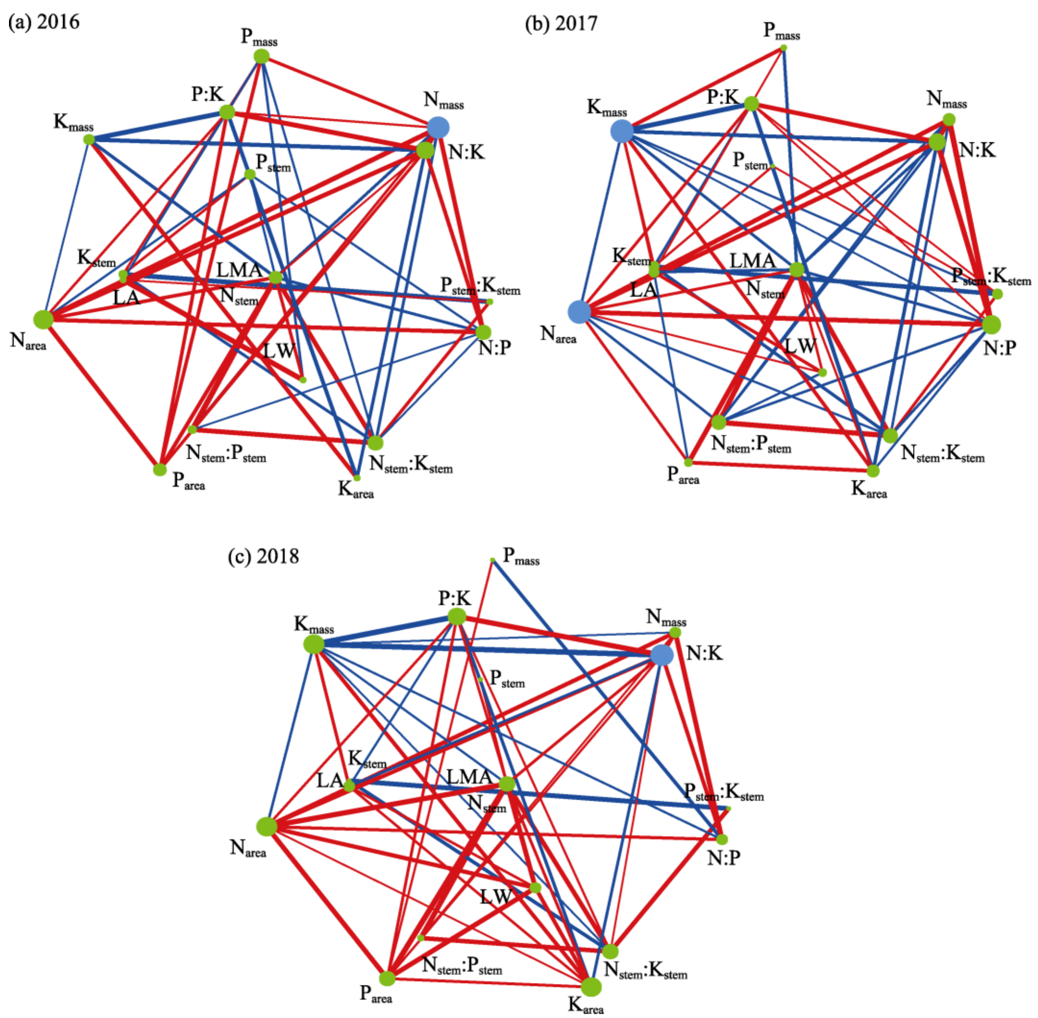

Fig. 6 Plant trait networks (PTNs) of declining wild apple trees sampled in 2016 (a), 2017 (b), and 2018 (c) in the Qiaolakesai Valley. Green nodes represent different plant traits, and node size shows degree. Red and blue lines indicate positive and negative correlations, respectively. The thickness of the line indicates the association strength. Blue solid circle indicates the hub trait.

3.5 Correlations between plant traits and environmental factors

Most soil physical-chemical variables exhibited significant (P<0.05) differences among the four elevations or the three years, and sampling plots at 1500 m presented the poorest soil quality (Table S5). No obvious regularity for soil physical-chemical variables was found among the three years. Further, no significant correlation was observed between elevation and any plant trait (Fig. 7). Except for EC, other soil physical-chemical variables had no significant correlations with leaf traits (81 out of 108), and stem N, P, and K presented relatively high correlations with soil physical-chemical variables (16 out of 27). High correlations of most twig traits (leaf traits and stem nutrient concentrations) with soil EC and three meteorological factors were detected. PC and DBP had robust correlations with most environmental factors. Mass- and area-based leaf P concentrations, P_{stem}, K_{stem}, and DBP were significantly (P<0.05) negatively correlated with AAP and MDT, while leaf N:P, LA, and PC were significantly (P<0.05) positively correlated with them. Soil EC showed the opposite trend with these two meteorological factors (AAP and MDT). MAT presented relatively weak impacts on plant traits. In general, MDT, AAP, and soil EC were highly correlated with the plant traits of declining wild apple trees.

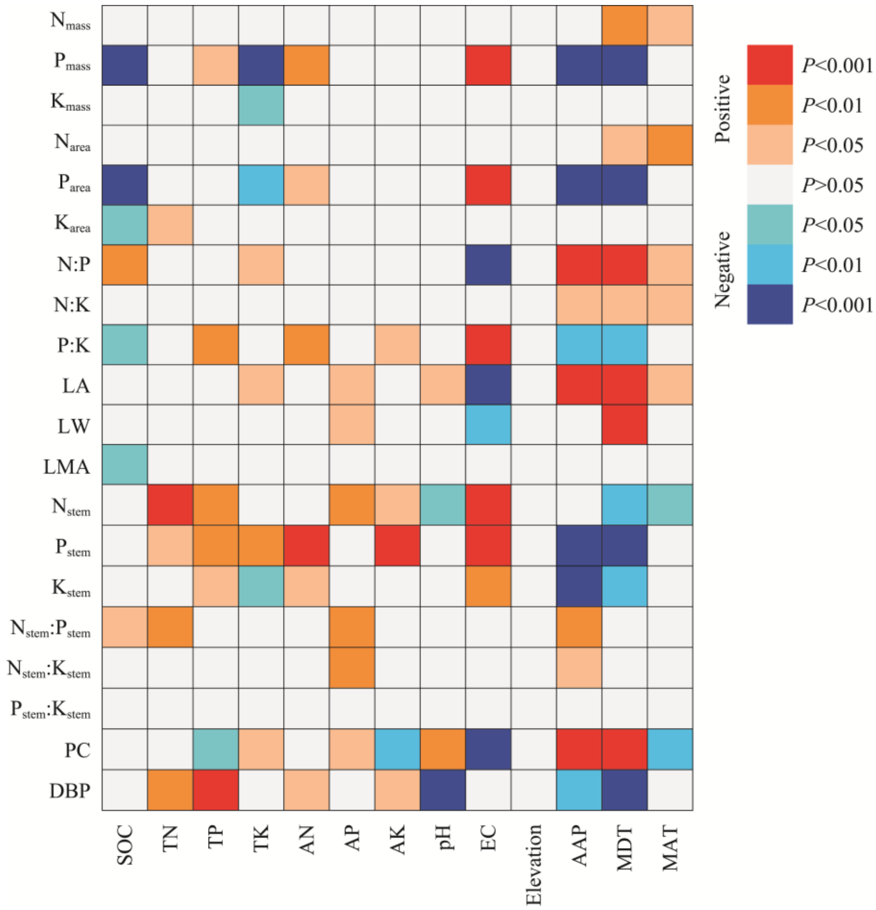

Fig. 7 Significance of correlation coefficient of environmental factors with PC, DBP, and twig traits of all declining wild apple trees sampled in the Qiaolakesai Valley. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; EC, electrical conductivity; AAP, annual accumulative precipitation; MDT, annual mean difference between day and night temperatures; MAT, mean annual temperature.

The non-metric multidimensional scaling results indicated that MDT (r=0.556), EC (r= –0.476), AAP (r=0.330), and pH (r=0.312) exhibited the highest correlations with the first axis (Axis 1) at P<0.001 level, followed by TP, MAT, TN, AK, and AN, indicating that Axis 1 mainly reflected the influence of meteorological factors and soil chemical properties (Table 2; Fig. S6). Further, high MDT, AAP, pH, and TK corresponded to high PC, LA, K_{mass}, and leaf N:P and low P_{mass}, P_{area}, P:K, LMA, N_{stem}, P_{stem}, and K_{stem}; however, the effects of EC, MAT, TN, TP, AN, and AK showed the opposite trend. In the second axis (Axis 2), AK (r=0.283), pH (r= –0.261), and EC (r=0.183) were significantly correlated with the axis (P<0.05), indicating that Axis 2 mainly reflected the influence of several soil variables. Among the 20 plant traits, PC and DBP were most affected by environmental factors, and their correlation coefficients with Axis 1 reached 0.921 and –0.934, respectively (P<0.001), followed by LA (r=0.483), P_{area} (r=0.345), P:K (r=0.338), P_{mass} (r=0.326), and P_{stem} (r=0.323) (P<0.001). According to the contribution of each environmental factor, the main influencing factors on plant trait matrix of declining wild apple trees were MDT, EC, AAP, and pH.

3.6 SEM explaining the variation in plant growth

Individual growth status was the comprehensive embodiment of various traits and functions of plant organs. The explanation of SEM model for the variation of individual growth vigor (expressed by PC) of declining wild apple trees was 41.9% (Fig. 8). MDT showed a significant

Table 2 Correlation coefficients of the first two axes of non-metric multidimensional scaling (NMDS) ordination with the environmental factors and plant traits of declining wild apple trees in the Qiaolakesai Valley

Environmental factor	Axis 1	Axis 2	Plant trait	Axis 1	Axis 2
AAP	0.330***	–0.135	N_{mass}	0.009	0.025
MAT	–0.253**	–0.015	P_{mass}	–0.326***	0.056
MDT	0.556***	–0.108	K_{mass}	0.251**	–0.391***
Elevation	–0.125	0.084	N_{area}	–0.154	0.039
SOC	0.023	0.072	P_{area}	–0.345***	0.063
TN	–0.221*	0.146	K_{area}	0.044	–0.294***
TP	–0.272**	0.172	N:P	0.193*	–0.019
TK	0.211*	–0.006	N:K	–0.129	0.178*
AN	–0.191*	0.156	P:K	–0.338***	0.213
AP	0.104	0.070	N_{stem}	–0.269**	0.196*
AK	–0.218*	0.283**	P_{stem}	–0.323***	0.197*
pH	0.312***	–0.261**	K_{stem}	–0.257**	0.098
EC	–0.476***	0.183*	N_{stem}: P_{stem}	–0.128	0.146
Variation explained	85.7%	6.6%	N_{stem}: K_{stem}	–0.098	0.174
			P_{stem}: K_{stem}	–0.048	0.161
			LA	0.483***	–0.078
			LW	0.147	–0.013
			LMA	–0.205*	0.036
			PC	0.921***	–0.649***
			DBP	–0.934***	0.672***

Note: Axis 1, the first axis of NMDS ordination; Axis 2, the second axis of NMDS ordination. SPC, projective coverage; DBP, dead branch percentage; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; EC, electrical conductivity; AAP, annual accumulative precipitation; MDT, annual mean difference between day and night temperatures; MAT, mean annual temperature. *, P<0.05 level; **, P<0.01 level; ***, P<0.001 level.

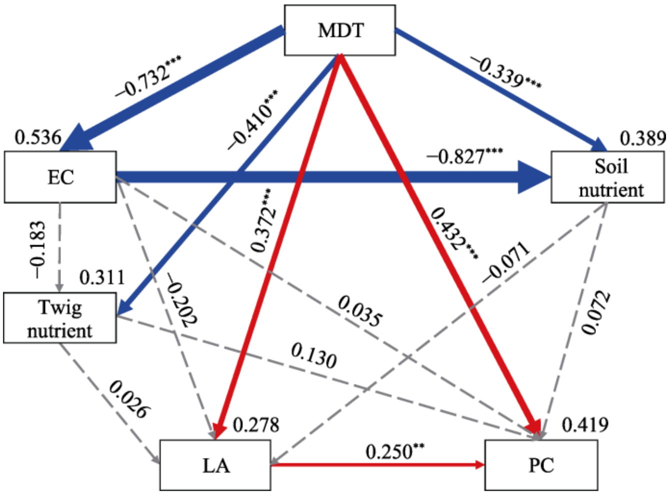

Fig. 8 Structural equation model (with standardized regression weights) depicting relative effects of meteorological factors, soil physical-chemical variables, twig nutrient, and LA on the plant growth status of declining wild apple trees in the Qiaolakesai Valley. The total amount of variance (R^2) explained for each endogenous variable (i.e., those with arrows pointing to them) is given on the top of the variable. Red and blue arrows indicate significant positive and negative relationships, respectively. Numbers adjacent to arrows are standardized path coefficients. The thickness of the arrows denotes the strength of these significant paths. Dotted arrows represent non-significant paths (P>0.05). **, P<0.01 level; ***, P<0.001 level. The fit of the model to the data is satisfactory (P=0.657, root mean square error of approximation (RMSEA)=0.000, χ^2=0.198, degree of freedom (df)=1, normed-fit index (NFI)=0.999, reporting fit index (RFI)=0.986, incremental fit index (IFI)=1.003, Tucker-Lewis index (TLI)=1.059, comparative fit index (CFI)=1.000, and Akaike information criterion (AIC)=52.198).

(P<0.001) negative direct effect on EC and soil nutrient, and EC presented a strong negative direct effect on soil nutrient. MDT also exhibited a significant (P<0.001) negative direct effect on twig nutrient. No significant effects of EC, soil nutrients, and twig nutrient on LA were detected, whereas MDT showed a significant (P<0.001) positive effect on LA. The variable PC was only directly affected by MDT and LA, in which MDT had a greater impact (standardized regression weight=0.432) than LA (standardized regression weight=0.250). MDT indirectly affected PC through LA. As such, the growth of declining wild apple trees was mainly directly driven by MDT.

4 Discussion

4.1 Elevational differences in the plant traits of declining wild apple trees

Different elevations may exhibit different dominant factors, and the elevational variability of plant growth and physiology also showed marked differences in different species, functional groups, and ecozones (Pellissier et al., 2010; Malinková et al., 2013; Wang et al., 2018; Gong et al., 2020). In the present study, with increasing elevation, PC generally increased whereas DBP decreased; that is, the growth of declining wild apple trees was relatively poor in high-elevation region in the study area. This effect may be related to the strong environmental stress caused by high elevation (Fang et al., 2004; Scheepens et al., 2010). Leaf size reflects the light interception efficiency of plants, and large leaves have high light acquisition efficiency (Liu and Ma, 2015; Lusk et al., 2019). Large leaves usually have long petioles and low leafing intensity (i.e., leaf number is relatively low), and leaves are arranged dispersedly in space (Niinements et al., 2006; Duursma et al., 2012; Smith et al., 2017; Li and Wang, 2021). Therefore, the self-shading between leaves becomes low, and the light acquisition area is relatively large for large leaves. In general, the sizes of plant leaves decrease with increasing elevation (Wang and Wang, 2015; Li et al., 2017; Li and Wang, 2021), mainly because the cost of respiration and transpiration of small leaves is low at low-temperature environment of high elevation, thus reducing plant energy consumption (Lambers, 2008; Scheepens et al., 2010). In addition, adverse environments, such as low temperature, can reduce water and nutrient transfer efficiency, therefore decreasing plant investment in leaves (Westoby et al., 2002). The pooled three-year data showed that LA at the highest elevation was the minimum (Fig. S2), which was in line with the general law (Wang and Wang, 2015; Li et al., 2017; Li and Wang, 2021). LMA can be used to reflect the carbon acquisition strategy of plants and has an important impact on the relative growth rate of plants (Wright et al., 2004; Milla and Reich, 2007). As elevation increases, meteorological conditions become worse while LMA increases (Scheepens et al., 2010; Wang and Wang, 2015). For instance, Hölscher et al. (2002) showed that the LMA values of four tree species in the north of Hesse, Germany, increased with increasing elevation. In our study, the LMA values of declining wild apple trees did not change significantly with increasing elevation, either alone or pooled for three-year data (Figs. 3 and S2), indicating that the carbon acquisition strategy of declining wild apple trees with different elevations was conservative to an extent.

Elevation usually remarkably affects plant nutrient concentration and nutrient utilization strategy. It is a common phenomenon that N_{area} in plant leaves increases with increasing elevation, but the response trend of N_{mass} to elevation is inconsistent (Cordell et al., 1999; Wang and Wang, 2015). Meta-analysis of TRY Plant Trait Database showed that the concentrations of N_{mass} and P_{mass} have remarkable upward trends with increasing elevation (Gong et al., 2020), but the results of different species or regions are not completely consistent. With increasing elevation, N_{mass} of *Leontopodium alpinum* decreases first and then increases; leaf N:P increases first, then decreases, and then increases again; and the change trend of P_{mass} is the opposite (Zhang et al., 2019). For dryland plants in the middle part of the Tianshan Mountains, leaf N:P decreases with increasing elevation, P_{mass} gradually increases, and N_{mass} shows no obvious change (Yang et al., 2017). With increasing elevation, N_{mass} of a woody gymnosperm *Cunninghamia lanceolata* gradually decreases, while P_{mass} first decreases and then increases (Chen et al., 2016). In this study, mass-

and area-based leaf N increased with increasing elevation in 2016 and 2018 but decreased in 2017. For the pooled three-year data of each elevation, except for K_{mass}, no significant elevational variability was found in mass- or area-based leaf N, P, and K concentrations. The same observation was found for N:P, N:K, and P:K, which showed the lowest values at 1500 m (Fig. S4). From the perspective of plant physiology, under stress environment, plants will allocate more N to increase proline and antioxidant enzymes, which can reduce plant water potential and then increase N concentration (Lambers, 2008). Based on the thresholds of leaf N_{mass} and P_{mass} concentrations and N:P ratio (Koerselman and Meuleman, 1996; Tao et al., 2020), for all elevations and years in this study, P_{mass} was higher than 1.00 mg/g, N_{mass} was lower than 20.00 mg/g, and N:P was less than 14.00, revealing that N limitation always existed in declining wild apple trees.

In addition, despite some differences between years, the pooled data indicated no significant correlation between elevation and the twig stoichiometric traits of declining wild apple trees (Fig. 7). This finding is contradictory to the "nutrient limitation" hypothesis, which holds that low soil temperature in high-elevation area limits plant root activity and reduces root nutrient absorption, resulting in nutrient limitation in high-elevation region (Reich and Oleksyn, 2004; Soethe et al., 2008). Temperature is not the only limiting factor determining leaf traits along an elevation. The range of elevation plays an important role in shaping leaf traits. Temperature can become a limiting factor for plant growth only when elevation reaches a certain height (Lebrija-Trejos et al., 2010). As one of the few deciduous broad-leaved tree species in Central Asia, the range of elevation in which wild apple trees are distributed in the Tianshan Mountains is limited because of their special environmental needs (Zhang et al., 2015), and thus plant and soil nutrients may be decoupled. Meanwhile, the existence of the inversion layer in this area (Zhang, 1973; Yan and Xu, 2010) may offset the comprehensive environmental stress caused by increase in elevation to a certain extent, and thus many twig traits of declining wild apple trees were obviously elevation independent.

Marked differences in genetic diversity of declining wild apple trees were found between elevations, and trees in middle-elevation region had the highest genetic diversity because of the gentle terrain in this area, which has suitable hydrothermal conditions and low degree of human interference (Zhang and Zheng, 2020). However, in this study, most leaf nutrient traits did not show maximum or minimum values in middle-elevation region (Fig. S4). The so-called environmental superiority of mid-elevation was not evident for most twig traits of declining wild apple trees. The possible reason was the narrow elevation range and unobvious environmental gradient.

4.2 Interannual differences in plant traits and the influencing factors

The growth status of declining wild apple trees differed markedly in different years, and the interannual difference was higher than the elevational difference. The growth vigor was the worst in 2016, but it was obviously improved in 2017 and 2018 (PC increased and DBP decreased). Differences in leaf size, leaf N_{mass} (or N_{area}), and N:P among different years were more obvious than those among different elevations. Compared with 2016, the leaves of declining wild apple trees became larger in 2017 and 2018, and leaf N_{mass}, N:P, and PC increased, indicating that the growth status of declining wild apple trees was improved, and the N limitation was alleviated to a certain extent (Figs. S3 and S5). Elevational variations in the growth vigor and leaf traits of declining wild apple trees in different years are apparently related to the interannual difference in meteorological factors (Wang and Wang, 2015; Du et al., 2021; Richmond et al., 2021).

Exploring the trait–trait correlations using PTN can improve our understanding of physiological and ecological rules regulating trait interactions among organs and plant growth under environmental stress (He et al., 2018; Kleyer et al., 2019; Rao et al., 2022). A network based on a dataset of 23 traits from 2530 individuals of 126 plant species from 381 plots in Northwest Europe has revealed that biomass allocation traits and stem specific length are hub traits in herbaceous perennial plants (Kleyer et al., 2019). Another study has indicated that the

trait relationships of broad-leaved trees are tighter than conifers, and the trait relationships of shrubs are tighter than trees; however, a general law that leaf N concentration and life span have the highest centrality in all leaf trait networks for these four vegetation types has been found (Li et al., 2022). Compared with healthy wild apple trees, seriously declining wild apple trees (mean DBP reached 64% and 75% in 2016 and 2017, respectively) can not only reduce nutrient content and leaf size but also change the PTN structure and hub traits (Yan et al., 2022). The hub traits in PTNs in this work differed completely in the three years (Fig. 5; Table S3), revealing that the varied environmental conditions in different years can lead to the change in the trait–trait associations and even the adjustment of environmental adaptation strategies for declining wild apple trees. The modularity of PTN in 2016 was higher than that in 2017 and 2018, indicating that relatively stronger functional decoupling existed in 2016 (Li et al., 2021; Rao et al., 2022). The lowest modularity of PTN in 2018 demonstrated that declining wild apple trees exhibited the strongest functional coupling in this year, that is, the growth status in 2018 was the best among the three years. This result was in consistent with the growth indicators and leaf traits (Figs. S3 and S5).

Robust associations among PC, DBP, and twig traits existed in this study. K_{mass} and N:P were evidently positively correlated with PC, whereas P_{mass}, P_{area}, P:K, N_{stem}, P_{stem}, and K_{stem} showed notably negative correlations with PC. DBP presented the opposite trend with PC (Table 2; Fig. S6). The results showed that the better the plant growth vigor is (i.e., higher PC and lower DBP), the larger the leaf size (i.e., the larger the effective photosynthetic area) and the lower the leaf and stem P and K concentrations are. Leaf P is closely related to the relative growth rate of plants, and high leaf P concentration corresponds to high relative growth rate (Sterner and Elser, 2002; Tian et al., 2018; Lambers, 2022). When plants encounter stress, they usually increase K concentration to improve stress resistance (Liu et al., 2006; Lo'ay et al., 2021). Therefore, the partial or massive death of tree branches under biological (e.g., *A. mali*) and abiotic (e.g., climate change) stresses would cause plant stress response (Zhang et al., 2020). This response would increase P concentration to promote the rapid growth of new vegetative branches in the trunks and thick branches of declining wild apple trees and increase K concentration to increase stress resistance. Thus, the twig stoichiometric characteristics of declining wild apple trees were notably correlated with their growth vigor.

Correlation analysis showed that AAP and MDT had basically the same effect on plant traits (Fig. 6). Increases in AAP and MDT evidently reduced leaf and stem P and K concentrations and increased their N:P and N:K ratios. Under this condition, the individual growth of declining wild apple tree was improved, and the leaf size increased (i.e., the larger effective photosynthetic area). Increase in AAP within a certain range is conducive to plant growth and productivity, which has been fully confirmed (Lambers, 2008). MDT was positively correlated with the leaf N concentration and N:P of declining wild apple trees but negatively correlated with stem N, indicating that the response of stem and leaf N to increase in MDT was opposite, that is, when MDT increased, stems would transport more N to leaves, thereby increasing leaf N concentration and decreasing stem N concentration.

Change in MDT has significant impact on vegetation productivity. A high MDT is conducive to the accumulation of organic matter for plants. For alpine shrubs on the Qinghai-Tibet Plateau of China, increase in MDT is conducive to the accumulation of organic matters and improves aboveground productivity (Zhu et al., 2020). A certain degree of MDT treatment can promote the bolting, budding, flowering, and flower bud differentiation of radishes, as well as axillary bud germination and branching, and the longer the treatment time is, the more obvious the promotion effect is (Pei et al., 2018). Appropriate low temperature and MDT contribute to the vegetative growth of *Lycoris radiata* (Cai et al., 2018). Narrowing diurnal temperature amplitude alters carbon trade-off and reduces the growth of C_4 crop Sorghum (Sunoj et al., 2016, 2020). Therefore, the decrease in MDT in future climate change (Chen et al., 2011; Li et al., 2021) may lead to a reduction in vegetation productivity (Zhu et al., 2019; Zang et al., 2020). This effect is

not good news for declining wild apple trees. Climate warming leads to increase in night temperature and decrease in MDT, and carbohydrates consumed by plants at night are difficult to be fully supplemented during the day. Trees will always be in a state of carbon starvation, which will further exacerbate the declining trend.

Plant stoichiometric characteristics generally have close correlation with soil factors, especially soil nutrients (Miatto et al., 2016; Zhang et al., 2017). In this work, soil nutrients presented different effects on the stoichiometric traits of current-year stems of declining wild apple trees. Increases in soil TN, TP, and AK contributed to increases in stem N and P concentrations, and EC promoted increases in stem N, P, and K concentrations, which was the same as the result of notable positive correlation between soil and plant nutrients in loess hilly area (Ru et al., 2016). The average soil pH value was 7.28 in the study area, close to the neutral soil. The overall correlation between soil pH and stem nutrients of declining wild apple trees was weak, which is different from the result showing a significant positive correlation between soil pH and leaf N concentration in *Picea schrenkiana* var. *tianschanica* in a high-elevation area (Li et al., 2019). Increase in AAP can notably reduce soil EC, thereby reducing the inhibition of salinity on soil enzyme activity and further contributing to the accumulation of soil available nutrients (Pankova and Konyushkova, 2013). However, from the perspective of SEM, increase in MDT was not conducive to soil nutrient accumulation, but this direct effect was lower than the indirect promotion effect of MDT on soil nutrients through EC (Fig. 8). LA and PC were directly and positively affected by MDT, which can indirectly influence PC through LA and further promote the growth vigor of plants. Soil physical-chemical variables and twig nutrients had no significant effect on the growth of declining wild apple trees. Meteorological factors might have weakened their action pathway and strength. Consequently, the results that SEM emphasized the direct impact of climate change on declining wild apple trees are worthy of attention.

5 Conclusions

The spatiotemporal changes and influencing factors of the growth status of declining wild apple trees in the Qiaolakesai Valley of the western Tianshan Mountains in Xinjiang were systematically analyzed in this study. We find that plant traits show differential response to elevation and year, and year exhibits higher impact than elevation. The N limitation on the growth vigor of plants exists in all three years (2016–2018). The hub traits differ in twig trait networks among different years, but the strength of twig functional coupling increases yearly. MDT, AAP, and soil pH present positive effects on the plant trait matrix, whereas soil EC, MAT, and several soil nutrient variables show negative effects. The meteorological factor MDT is the direct driver of the growth of declining wild apple trees in the study area. These results confirm that the natural populations of wild apple trees in valley habitats are still facing marked declining pressure under potential climate change. It is suggested to strengthen the research on the impact of climate change, especially MDT change, on the growth of declining wild apple trees in the Tianshan Mountains in the future.

Acknowledgements

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research (STEP) Program (2019QZKK0502), the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA2005020402), the Youth Innovation Promotion Association Project, Chinese Academy of Sciences (Y201976), and the National Science and Technology Basic Program of China (2019FY100204). We would like to thank the editors and reviewers for their valuable insights and constructive comments. We are grateful to Ms. Maziyirea NUERHAILATI, Dr. LU Yongxing, and Dr. SUN Yixiang from Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, and Mr. LIU Xinghua and Mr. WANG Jianyong from Yili Botanical Garden, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences for their kindly help in field work. We also thank Dr. GONG Yanming, Dr. LI Yonggang, Dr. YIN Benfeng, and Mr. ZHANG Shihang from Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences for their valuable suggestions in data analyses.

References

Bao S D. 2000. Analysis of Soil and Agrochemistry (3rd ed.). Beijing: China Agriculture Press, 25–144. (in Chinese)

Cai J H, Wei X Y, Li J F, et al. 2018. The regulation and control of ambient temperature on growth rhythm of *Lycoris radiata*. Acta Agriculturae Universitatis Jiangxiensis, 40(1): 24–31. (in Chinese)

Chen C, Wang G J, Zhao Y, et al. 2016. Seasonal dynamics and allometric growth relationships of C, N, and P stoichiometry in the organs of *Cunninghamia lanceolata* from Huitong. Acta Ecologica Sinica, 36(23): 7614–7623. (in Chinese)

Chen F H, Huang W, Jin L Y, et al. 2011. Spatiotemporal precipitation variations in the arid Central Asia in the context of global warming. Science China-Earth Sciences, 54(12): 1812–1821.

Chen X S, Mao Z Q, Wang N, et al. 2021. Progress on evaluation, mining and utilization of germplasm resource of deciduous fruit trees in Xinjiang. Journal of Plant Genetic Resources, 2(6): 1483–1490. (in Chinese)

Cordell S, Goldstein G, Meinzer F C, et al. 1999. Allocation of nitrogen and carbon in leaves of *Metrosideros polymorpha* regulates carboxylation capacity and δ^{13}C along an altitudinal gradient. Functional Ecology, 13(6): 811–818.

Cui Z J, Zhang Y L, Zhang X, et al. 2019. Life history and mortality factors of *Agrilus mali* Matsumura (Coleoptera: Buprestidae) in wild apples in Northwestern China. Agricultural and Forest Entomology, 21(3): 309–317.

Du B M, Ji H W, Liu C J. 2021. Nutrient resorption strategies of three oak tree species in response to interannual climate variability. Forest Ecosystems, 8: 70, doi: 10.1186/s40663-021-00350-8.

Duan N B, Bai Y, Sun H H, et al. 2017. Genome re-sequencing reveals the history of apple and supports a two-stage model for fruit enlargement. Nature Communications, 8: 249, doi: 10.1038/s41467-017-00336-7.

Duursma R A, Falster D S, Valladares F, et al. 2012. Light interception efficiency explained by two simple variables: A test using a diversity of small- to medium-sized woody plants. New Phytologist, 193(2): 397–408.

Falster D S, Duursma R A, FitzJohn R G. 2018. How functional traits influence plant growth and shade tolerance across the life cycle. Proceedings of the National Academy of Sciences, 115(29): E6789–E6798.

Fang J Y, Shen Z H, Cui H T. 2004. Ecological characteristics of mountains and research issues of mountain ecology. Biodiversity Science, 12(1): 10–19. (in Chinese)

Flores-Moreno H, Fazayeli F, Banerjee A, et al. 2019. Robustness of trait connections across environmental gradients and growth forms. Global Ecology and Biogeography, 28(12): 1806–1826.

Gong H D, Li Y Y, Yu T, et al. 2020. Soil and climate effects on leaf nitrogen and phosphorus stoichiometry along elevational gradients. Global Ecology and Conservation, 23: e01138, doi: 10.1016/j.gecco.2020.e01138.

Han W X, Fang J Y, Reich P, et al. 2011. Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China. Ecology Letters, 14 (8): 788–796.

He N P, Liu C C, Zhang J H, et al. 2018. Perspectives and challenges in plant traits: From organs to communities. Acta Ecologica Sinica, 38(19): 6787–6796. (in Chinese)

He N P, Li Y, Liu C C, et al. 2020. Plant trait networks: improved resolution of the dimensionality of adaptation. Trends Ecology and Evolution, 35(10): 908–918.

He Y Y, Guo S L, Wang Z. 2019. Research progress of trade-off relationships of plant functional traits. Chinese Journal of Plant Ecology, 43(12): 1021–1035.

Hölscher D, Schmitt S, Kupfer K. 2002. Growth and leaf traits of four broad-leaved tree species along a hillside gradient. Forstwiss Centralbl, 121(5): 229–239.

Hu R J. 2004. Physical Geography of the Tianshan Mountains in China. Beijing: China Environmental Publishing House, 52–101. (in Chinese)

Kleyer M, Trinogga J, Cebrián-Piqueras M A, et al. 2019. Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. Journal of Ecology, 107(2): 829–842.

Kline R B. 2010. Principles and Practice of Structural Equation Modeling (3rd ed.). New York: Guilford Press, 231–365.

Koerselman W, Meuleman A F. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. Journal of Applied Ecology, 33(6): 1441–1450.

Lambers H, Chapin F S, Pons T L. 2008. Plant Physiological Ecology (2nd ed.). New York: Springer, 11–90.

Lambers H. 2022. Phosphorus acquisition and utilization in plants. Annual Review of Plant Biology, 73: 17–42.

Lebrija-Trejos E, Pérez-García E A, Meave J A, et al. 2010. Functional traits and environmental filtering drive community

assembly in a species-rich tropical system. Ecology, 91(2): 386–398.

Li H W, Li Z, Chen Y N, et al. 2021. Projected meteorological drought over Asian drylands under different CMIP6 scenarios. Remote Sensing, 13(21): 4409, doi: 10.3390/rs13214409.

Li X, Pei K, Kéry M, et al. 2017. Decomposing functional trait associations in a Chinese subtropical forest. PLoS ONE, 12(4): e0175727, doi: 10.1371/journal.pone.0175727.

Li X F, Li L, Chang Y P, et al. 2019. Stoichiometric characteristics of leaf C and N and their correlation with soil physicochemical factors in *Picea Schrenkiana* forests. Arid Land Geography, 42(3): 599–605. (in Chinese)

Li Y, Liu C C, Xu L, et al. 2021. Leaf trait networks based on global data: representing variation and adaptation in plants. Frontiers in Plant Science, 12: 2728, doi: 10.3389/fpls.2021.710530.

Li Y, Liu C C, Sack L, et al. 2022. Leaf trait network architecture shifts with species-richness and climate across forests at continental scale. Ecology Letters, 25(6): 1442–1457.

Li Y Q, Wang Z H. 2021. Leaf morphological traits: Ecological function, geographic distribution and drivers. Chinese Journal of Plant Ecology, 45(10): 1154–1172.

Liao L, Zhang W H, Zhang B, et al. 2021. Unraveling a genetic roadmap for improved taste in the domesticated apple. Molecular Plant, 14(9): 1454–1471.

Liu X J, Ma K P. 2015. Plant functional traits-concepts, applications and future directions. Scientia Sinica Vitae, 45(4): 325–339.

Liu X Y, He P, Jin J Y. 2006. Advances in effect of potassium nutrition on plant disease resistance and its mechanism. Plant Nutrition and Fertilizer Science, 12(3): 445–450. (in Chinese)

Lo'ay A A, EL-Ezz S F A, Awadeen A A. 2021. Effect of different foliar potassium fertilization forms on vegetative growth, yield, and fruit quality of kaki trees grown in sandy soil. Scientia Horticulturae, 288: 110420, doi: 10.1016/j.scienta.2021.110420.

Luo Y, Peng Q W, Li K H, et al. 2021. Patterns of nitrogen and phosphorus stoichiometry among leaf, stem and root of desert plants and responses to climate and soil factors in Xinjiang. CATENA, 199: 105100, doi: 10.1016/j.catena.2020.105100.

Lusk C H, Grierson E R P, Laughlin D C. 2019. Large leaves in warm, moist environments confer an advantage in seedling light interception efficiency. New Phytologit, 223(3): 1319–1327.

Malinková E, Kukla J, Kuklová M, et al. 2013. Altitudinal variation of plant traits: Morphological characteristics in *Fragaria vesca* L. (Rosaceae). Annals of Forest Research, 56(1): 79–89.

McCune B, Mefford M J. 2011. PC-ORD. Multivariate Analysis of Ecological Data (Version 6). MjM Software, Gleneden Beach, Oregon, USA.

Mendes M R A, Silva Júnior M C, Castro A A J F, et al. 2014. Temporal change in species and functional plant traits in the moist grassland on the Sete Cidades National Park, Piauí, Brazil. Brazilian Journal of Biology, 74(1): 111–123.

Milla R, Reich P B. 2007. The scaling of leaf area and mass: The cost of light interception increases with leaf size. Proceedings of the Royal Society B-Biological Sciences, 274(1622): 2109–2114.

Niinements U, Portsmuth A, Tobias M. 2006. Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. New Phytologist, 171(1): 91–104.

Pankova E I, Konyushkova M V. 2013. Climate and soil salinity in the deserts of Central Asia. Eurasian Soil Science, 46(7): 721–727.

Pei Y, Zhang C S, Tian S J, et al. 2018. Effect of different diurnal temperature changes on bolting and flowering properties of radish (*Raphanus sativus* L.). Northern Horticulture, 42(11): 1–8. (in Chinese)

Pellissier L, Fournier B, Vittoz G P. 2010. Plant traits co-vary with altitude in grasslands and forests in the European Alps. Plant Ecology, 211(2): 351–365.

Pérez-Camacho L, Rebollo S, Hernández-Santana V, et al. 2012. Plant functional trait responses to interannual rainfall variability, summer drought and seasonal grazing in Mediterranean herbaceous communities. Functional Ecology, 26(3): 740–749.

Rao Q Y, Su H J, Ruan L W, et al. 2022. Phosphorus enrichment affects trait network topologies and the growth of submerged macrophytes. Environmental Pollution, 292(Part A): 118331, doi: 10.1016/j.envpol.2021.118331.

Reich P B, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences, 101(30): 11001–11006.

Richmond I C, Leroux S J, Heckford T R, et al. 2021. Temporal variation and its drivers in the elemental traits of four boreal plant species. Journal of Plant Ecology, 14(3): 398–413.

Ru H L, Zhang H D, Jiao F, et al. 2016. Plant and soil C, N, P stoichiometric characteristics in relation to micro-topography in the Hilly Loess Plateau region, China. Journal of Natural Resources, 31(10): 1752–1763. (in Chinese)

Scheepens J F, Frei E S, Stöcklin J. 2010. Genotypic and environmental variation in specific leaf area in a widespread alpine plant after transplantation to different altitudes. Oecologia, 164(1): 141–150.

Smith D D, Sperry J S, Adler F R. 2017. Convergence in leaf size versus twig leaf area scaling: Do plants optimize leaf area partitioning? Annuls of Botany, 119(3): 447–456.

Soethe N, Lehmann J, Engels C. 2008. Nutrient availability at different altitudes in a tropical montane forest in Ecuador. Journal of Tropical Ecology, 24(4): 397–406.

Song L L, Fan J W, Wu S H. 2011. Research advances on changes of leaf traits along an altitude gradient. Progress in Geography, 30(11): 1431–1439. (in Chinese)

Spengler R N. 2019. Origins of the apple: The role of megafaunal mutualism in the domestication of *Malus* and Rosaceous trees. Frontiers in Plant Science, 10: 617, doi: 10.3389/fpls.2019.00617.

Sterner R W, Elser J J. 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton: Princeton University Press, 44–78.

Su Z H, Li W J, Cao Q M, et al. 2019. Age composition and quantitative dynamic status of *Malus sieversii* population. Arid Zone Research, 36(5): 1153–1160. (in Chinese)

Sunoj V S J, Shroyer K J, Jagadish S V K, et al. 2016. Diurnal temperature amplitude alters physiological and growth response of maize (*Zea mays* L.) during the vegetative stage. Environmental and Experimental Botany, 130: 113–121.

Sunoj V S J, Prasad P V V, Ciampitti I A, et al. 2020. Narrowing diurnal temperature amplitude alters carbon tradeoff and reduces growth in C_4 crop sorghum. Frontiers in Plant Science, 11: 1262, doi: 10.3389/fpls.2020.01262.

Tao Y, Nuerhailati M, Zhang Y M, et al. 2020. Influence of branch death on leaf nutrient status and stoichiometry of wild apple trees (*Malus sieversii*) in the Western Tianshan Mountains, China. Polish Journal of Ecology, 68(4): 296–312.

Tian D, Yan Z B, Niklas K J, et al. 2018. Global leaf nitrogen and phosphorus stoichiometry and their scaling exponent. National Science Review, 5(5): 728–739.

van de Weg M J, Meir P, Grace J, et al. 2009. Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along an Amazon-Andes gradient in Peru. Plant Ecology and Diversity, 2(3): 243–254.

Wang A, Xue W, Tognetti R, et al. 2018. Elevation alters carbon and nutrient concentrations and stoichiometry in *Quercus aquifolioides* in southwestern China. Science of the Total Environment, 622–623: 1463–1475.

Wang C S, Wang S P. 2015. A review of research on responses of leaf traits to climate change. Chinese Journal of Plant Ecology, 39(2): 206–216. (in Chinese)

Wang N, Jiang S H, Zhang Z Y, et al. 2018. *Malus sieversii*: the origin, flavonoid synthesis mechanism, and breeding of red-skinned and red-fleshed apples. Horticulture Research, 5: 70, doi: 10.1038/s41438-018-0084-4.

Wang Y D, Wei I S, Zhou M, et al. 2021. Ecological of stoichiometric characteristics of *Populus davidiana* forests with different growth and decline degrees in southern Daxing'anling. Chinese Journal of Soil Science, 52(4): 854–864. (in Chinese)

Westoby M, Falster D S, Moles A T, et al. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology Evolution and Systematics, 33(1): 125–159.

Westoby M, Wright I J. 2003. The leaf size-twig size spectrum and its relationship to other important spectra of variation among species. Oecologia, 135(4): 621–628.

Wright I J, Reich P B, Westoby M, et al. 2004. The world-wide leaf economics spectrum. Nature, 428(6985): 821–827.

Xiong J W. 2017. Comprehensive Scientific Investigation of the Western Tianshan Mountains in Xinjiang. Beijing: China Forestry Press, 1–128. (in Chinese)

Yan G R, Xu Z. 2010. Study on the Wild Fruit Trees in Xinjiang, China. Beijing: China Forestry Publishing House, 1–48. (in Chinese)

Yan J M, Zhou X B, Tao Y, et al. 2021. Variation in one-year-old branch stoichiometry of *Malus sieversii* at different altitudes and the influencing factors in Tianshan Mountains, China. Arid Zone Research, 38(2): 450–459. (in Chinese)

Yan J M, Li Y G, Maisupova B, et al. 2022. Effects of growth decline on twig functional traits of wild apple trees in two long-term monitoring plots in Yili Valley: Implication for their conservation. Global Ecology and Conservation, 33: e01998,

doi: 10.1016/j.gecco.2021.e01998.

Yang D M, Niklas K J, Xiang S, et al. 2010. Size-dependent leaf area ratio in plant twigs: Implication for leaf size optimization. Annuals of Botany, 105(1): 71–77.

Yang S Q, Zhao X J, Sen D, et al. 2017. Leaf C, N and P chemometries and their altitudinal variations in the central Tianshan Mountains. Arid Zone Research, 34(6): 1371–1379. (in Chinese)

Yao F Y, Chen Y H, Yan Z B, et al. 2015. Biogeographic patterns of structural traits and C:N:P stoichiometry of tree twigs in China's forests. PLoS ONE, 10: e0116391, doi: 10.1371/journal.pone.0116391.

Zang Y X, Min X J, de Dios V R, et al. 2020. Extreme drought affects the productivity, but not the composition, of a desert plant community in Central Asia differentially across microtopographies. Science of the Total Environment, 717: 137251, doi: 10.1016/j.scitotenv.2020.137251.

Zar J H. 2009. Biostatistical Analysis (5th ed.). Upper Saddle River, NJ: Prentice Hall, 91–293.

Zhang D, Wang C, Li X L, et al. 2017. Linking plant ecological stoichiometry with soil nutrient and bacterial communities in apple orchards. Applied Soil Ecology, 128: 1–10.

Zhang D Y, Peng Y F, Li F, et al. 2021. Changes in above-/below-ground biodiversity and plant functional composition mediate soil respiration response to nitrogen input. Functinal Ecology, 35(5): 1171–1182.

Zhang H X, Zhang M L, Ma L N. 2015. Genetic structure and historical demography of *Malus sieversii* in the Yili Valley and the western mountains of the Junggar Basin, Xinjiang, China. Journal of Arid Land, 7(2): 264–271.

Zhang H X, Zheng T Y. 2020. Effects of elevation on population genetic characteristics of *Malus sieversii*. Chinese Journal of Ecology, 39(12): 4031–4037. (in Chinese)

Zhang H X, Li X S, Wang J C, et al. 2021. Insights into the aridification history of Central Asian Mountains and international conservation strategy from the endangered wild apple tree. Journal of Biogeography, 48(2): 332–344.

Zhang K Y, Yang D, Zhang Y B, et al. 2021. Differentiation in stem and leaf traits among sympatric lianas, scandent shrubs and trees in a subalpine cold temperate forest. Tree Physiology, 41(11): 1992–2003.

Zhang P, Lyu Z Z, Zhang X, et al. 2019. Age structure of *Malus sieversii* population in Ili of Xinjiang and Kazakhstan. Arid Zone Research, 36(4): 844–853. (in Chinese)

Zhang P, Cui Z J, Xu H, et al. 2020. Thirst or malnutrition: The impacts of invasive insect *Agrilus mali* on the physiological status of wild apple trees. Forests, 11(4): 440, doi: 10.3390/f11040440.

Zhang X, Zhang Y L, Zhang P, et al. 2021. *Agrilus mali* Matsumura (Coleoptera: Buprestidae) density and damage in wild apple *Malus sieversii* (Rosales: Rosaceae) forests in Central Eurasia under four different management strategies. Entomologia Generalis, 41(3): 257–266.

Zhang X F, Liu X D, Jing W M, et al. 2019. Characteristics of *Leontopodium leontopodioides* leaf stoichiometry with altitude and their relationship with soil nutrients in Qilian Mountains, Northwest China. Chinese Journal of Applied Ecology, 30(12): 4012–4020. (in Chinese)

Zhang X S. 1973. On the eco-geographical characters and the problems of classification of the wild fruit-tree forest in the Ili Valley of Sinkiang. Acta Botanica Sinica, 15(2): 239–253. (in Chinese)

Zhu J B, He H D, Zhang F W, et al. 2020. Effect of temperature difference between day and night on NEE and its variation charactristics in Alpine shrubland in Qinghai-Tibetan Plateau. Research of Soil and Water Conservation, 27(4): 232–238. (in Chinese)

Zhu Y K, Zhang J T, Zhang Y Q, et al. 2019. Responses of vegetation to climatic variations in the desert region of northern China. CATENA, 175: 27–36.

Appendix

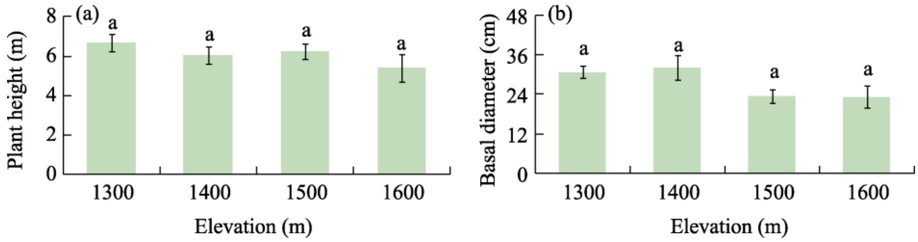

Fig. S1 Plant height (a) and basal diameter (b) of declining wild apple trees at different elevations in the Qiaolakesai Valley in 2016. Different lowercase letters indicate significant differences among the four elevations (P<0.05).

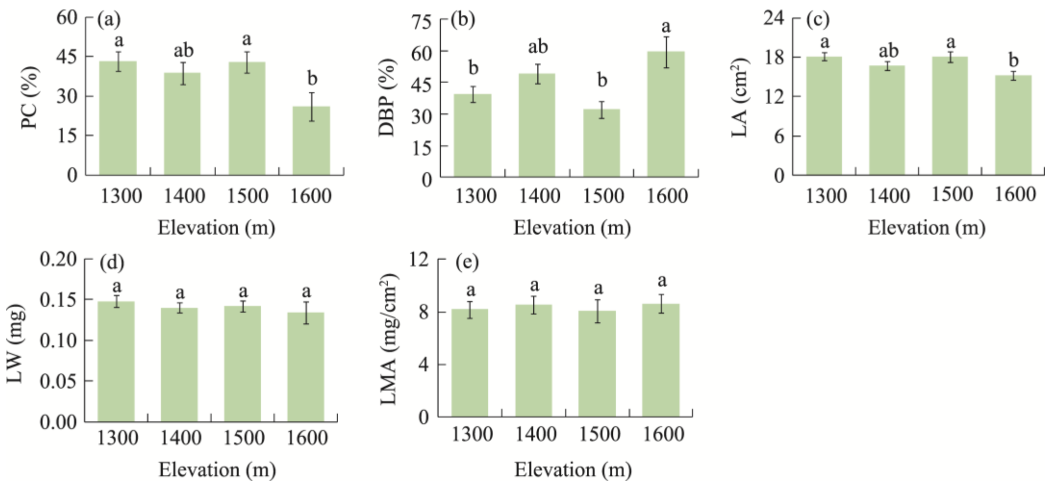

Fig. S2 Differences in projective coverage (PC; a), dead branch percentage (DBP; b), individual leaf area (LA; c), individual leaf weight (LW; d), and leaf mass per area (LMA; e) of declining wild apple trees at different elevations in the Qiaolakesai Valley in 2016. Different lowercase letters indicate significant differences among the four elevations (P<0.05).

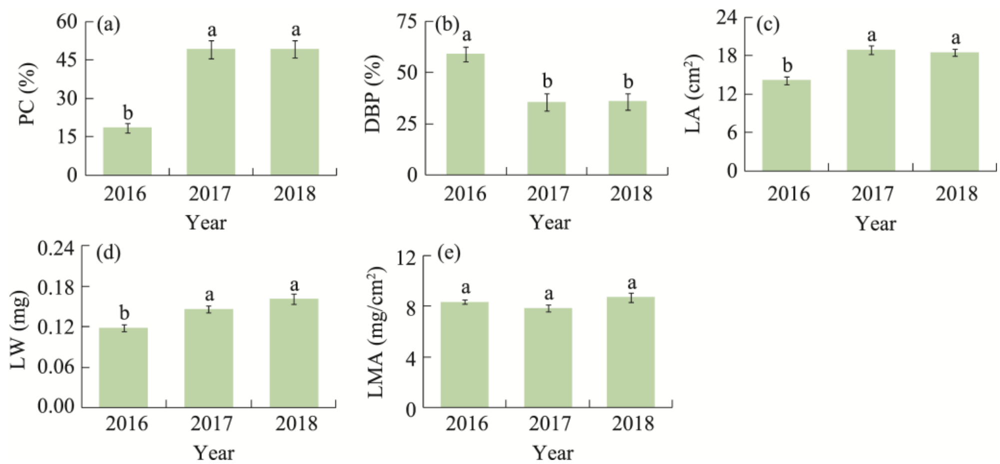

Fig. S3 Differences in PC (a), DBP (b), LA (d), LW (d), and LMA (e) of declining wild apple trees among the three years in the Qiaolakesai Valley. Different lowercase letters indicate significant differences among the three years (P<0.05).

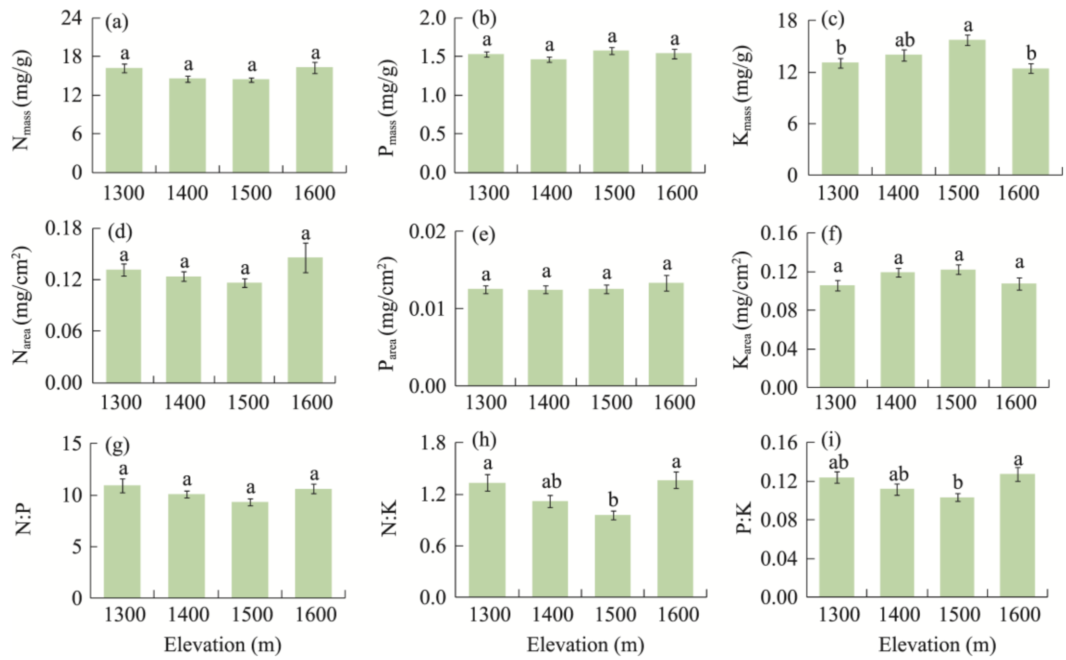

Fig. S4 Differences in leaf N_{mass}, P_{mass}, and K_{mass} concentrations (a, b, and c), leaf N_{area}, P_{area}, and K_{area} concentrations (d, e, and f), and leaf stoichiometric ratios (g, h, and i) of declining wild apple trees at different elevations in the Qiaolakesai Valley. N, nitrogen; P, phosphorus; K, potassium. N_{mass}, P_{mass}, and K_{mass} indicate leaf N, P, and K concentrations per unit mass, respectively. N_{area}, P_{area}, and K_{area} indicate leaf N, P, and K concentrations per unit area, respectively. Different lowercase letters indicate significant differences among the four elevations (P<0.05).

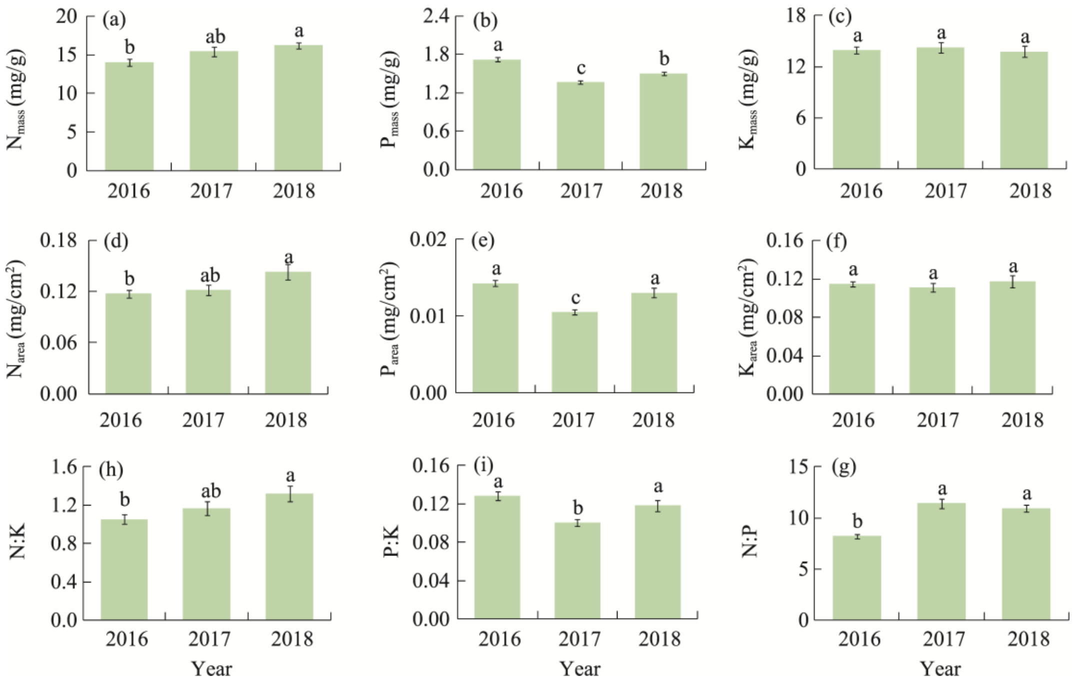

Fig. S5 Differences in leaf N_{mass}, P_{mass}, and K_{mass} concentrations (a, b, and c), leaf N_{area}, P_{area}, and K_{area} concentrations (d, e, and f), and the stoichiometric ratios (g, h, and i) of declining wild apple trees among three years in the Qiaolakesai Valley. Different lowercase letters indicate significant differences among the three years (P<0.05).

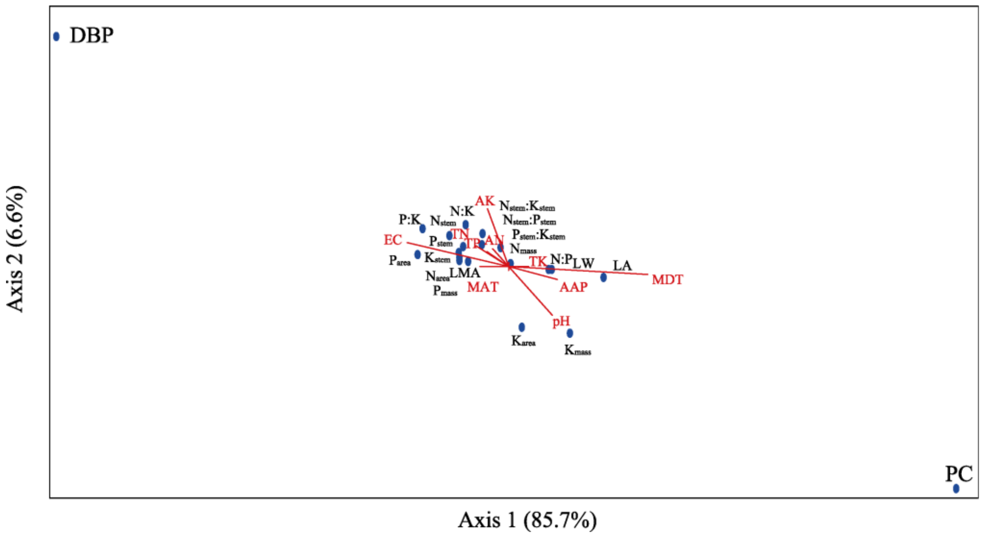

Fig. S6 Non-metric multidimensional scaling (NMDS) ordination diagram of environmental factors and plant traits of declining wild apple trees in the Qiaolakesai Valley. Axis 1, the first axis of NMDS ordination; Axis 2, the second axis of NMDS ordination. TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AK, available potassium; EC, electrical conductivity; AAP, annual accumulative precipitation; MDT, annual mean difference between day and night temperatures; MAT, mean annual temperature.

Table S1 Coefficients of variation for 20 plant traits of declining wild apple trees in the Qiaolakesai Valley

	PC	DBP	N_{mass}	P_{mass}	K_{mass}	N_{area}	P_{area}	K_{area}	N:P	N:K
Coefficient of variation	0.61	0.61	0.22	0.16	0.26	0.35	0.26	0.26	0.26	0.39
	P:K	LA	LW	LMA	N_{stem}	P_{stem}	K_{stem}	N_{stem}:P_{stem}	N_{stem}:K_{stem}	P_{stem}:K_{stem}
Coefficient of variation	0.28	0.25	0.30	0.22	0.26	0.15	0.23	0.25	0.33	0.19

Note: PC, projective coverage; DBP, dead branch percentage; N, nitrogen; P, phosphorus; K, potassium. N_{mass}, P_{mass}, and K_{mass} indicate leaf N, P, and K concentrations per unit mass, respectively. LA, individual leaf area; LW, individual leaf weight; LMA, leaf mass per unit area. N_{area}, P_{area}, and K_{area} indicate leaf N, P, and K concentrations per unit area, respectively. N_{stem}, P_{stem}, and K_{stem} indicate stem N, P, and K concentrations per unit mass, respectively.

Table S2 Differences in the current-year stem stoichiometric parameters of declining wild apple trees among different elevations or years in the Qiaolakesai Valley

Elevation (m)	N_{stem} (mg/g)	P_{stem} (mg/g)	K_{stem} (mg/g)	N_{stem}:P_{stem}	N_{stem}:K_{stem}	P_{stem}:K_{stem}
1300	6.89±0.35^{ab}	1.28±0.04^{a}	5.06±0.20^{a}	5.36±0.18^{ab}	1.41±0.08^{a}	0.26±0.01^{a}
1400	7.33±0.30^{a}	1.24±0.03^{a}	4.90±0.16^{a}	5.98±0.23^{a}	1.53±0.07^{a}	0.26±0.01^{a}
1500	6.31±0.27^{b}	1.27±0.03^{a}	4.86±0.18^{a}	5.06±0.25^{b}	1.36±0.08^{a}	0.27±0.01^{a}
1600	6.65±0.35^{ab}	1.22±0.04^{a}	5.02±0.31^{a}	5.54±0.33^{ab}	1.43±0.12^{a}	0.26±0.01^{a}
Year	N_{stem} (mg/g)	P_{stem} (mg/g)	K_{stem} (mg/g)	N_{stem}:P_{stem}	N_{stem}:K_{stem}	P_{stem}:K_{stem}
2016	7.28±0.30^{a}	1.40±0.03^{a}	5.43±0.17^{a}	5.30±0.21^{b}	1.40±0.07^{ab}	0.27±0.01^{a}
2017	6.71±0.27^{ab}	1.13±0.02^{c}	4.38±0.13^{b}	5.98±0.24^{a}	1.58±0.07^{a}	0.26±0.01^{a}
2018	6.35±0.23^{b}	1.23±0.02^{b}	5.03±0.18^{a}	5.17±0.17^{b}	1.32±0.07^{b}	0.25±0.01^{a}

Note: Different lowercase letters within the same column indicate significant (P<0.05) differences among different elevations or years (Yan et al., 2021).

Table S3 Topological properties of plant trait networks (PTNs) of declining wild apple trees in different years in the Qiaolakesai Valley

Topological property	2016	2017	2018
Edge number	43	50	47
Node number	18	18	18
Connectance	0.281	0.327	0.307
Average degree	4.778	5.556	5.222
Average path length	2.000	1.869	2.007
Edge connectivity	3	2	2
Clustering coefficient	0.464	0.484	0.560
Centralization betweenness	0.183	0.221	0.247
Centralization degree	0.248	0.261	0.281
Modularity	0.313	0.310	0.259

Table S4 Node (plant trait) properties of PTNs of declining wild apple trees in different years in the Qiaolakesai Valley

Trait	2016		2017		2018	
	Degree	Betweenness	Degree	Betweenness	Degree	Betweenness
N_{mass}	$9^{\#}$	31.950	4	1.243	4	7.783
P_{mass}	5	16.017	3	0.000	2	0.333
K_{mass}	4	2.083	$10^{\#}$	35.712	6	1.867
N_{area}	6	2.900	$10^{\#}$	27.521	9	10.233
P_{area}	6	2.767	3	0.200	7	10.267
K_{area}	3	0.000	5	3.200	9	16.150
N:P	4	1.583	7	3.093	5	6.267
N:K	8	12.933	8	7.500	$10^{\#}$	29.483
P:K	7	11.550	7	9.567	8	15.883
LA	2	2.033	4	1.583	5	1.333
LW	3	10.800	3	0.950	5	0.867
LMA	6	19.283	7	9.450	6	1.000
N_{stem}	5	6.317	6	3.886	3	4.533
P_{stem}	3	5.750	2	0.000	2	3.983
K_{stem}	4	7.433	5	9.176	2	0.000
N_{stem}:P_{stem}	3	0.000	5	1.243	3	3.783
N_{stem}:K_{stem}	5	13.867	6	9.500	6	40.233
P_{stem}:K_{stem}	3	5.733	5	9.176	2	0.000

Note: # indicates the trait with the highest degree in a PTN.

Table S5 Differences in soil physical-chemical variables in sampling plots of declining wild apple trees among different elevations or years in the Qiaolakesai Valley

Elevation (m)	SOC (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)	AN (mg/kg)	AP (mg/kg)	AK (mg/kg)	pH	EC (μS/cm)
1300	78.31 ±4.51[a]	6.57 ±0.36[a]	1.17 ±0.01[b]	21.18 ±0.11[a]	447.23 ±19.07[a]	12.38 ±0.44[a]	476.76 ±24.56[a]	7.55 ±0.04[a]	262.33 ±19.12[ab]
1400	92.88 ±6.90[a]	7.02 ±0.39[a]	1.15 ±0.02[b]	20.79 ±0.13[ab]	461.18 ±32.77[a]	11.56 ±0.59[a]	444.17 ±16.48[a]	6.96 ±0.08[b]	323.08 ±26.17[a]
1500	48.28 ±5.85[b]	3.58 ±0.23[b]	0.94 ±0.01[c]	20.61 ±0.23[b]	313.35 ±39.36[b]	7.84 ±0.84[b]	366.17 ±8.87[b]	7.73 ±0.06[a]	196.05 ±10.63[b]
1600	98.58 ±6.33[a]	7.58 ±0.29[a]	1.24 ±0.05[a]	20.31 ±0.18[b]	488.92 ±49.39[a]	12.07 ±0.63[a]	504.86 ±13.90[a]	6.63 ±0.08[c]	239.17 ±21.99[b]
Year	SOC (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)	AN (mg/kg)	AP (mg/kg)	AK (mg/kg)	pH	EC (μS/cm)
2016	66.26 ±4.62[b]	6.67 ±0.47[a]	1.18 ±0.04[a]	20.34 ±0.15[b]	505.90 ±33.22[a]	9.56 ±0.75[b]	479.29 ±22.40[a]	7.14 ±0.11[a]	389.57 ±16.22[a]
2017	109.74 ±6.23[a]	5.78 ±0.33[a]	1.04 ±0.02[b]	21.44 ±0.14[a]	287.53 ±24.95[b]	10.00 ±0.46[b]	371.14 ±8.95[b]	7.39 ±0.07[a]	153.46 ±5.05[c]
2018	56.34 ±3.30[b]	5.60 ±0.28[a]	1.11 ±0.01[ab]	20.52 ±0.11[b]	465.88 ±26.02[a]	12.83 ±0.56[a]	471.30 ±11.09[a]	7.31 ±0.07[a]	228.45 ±10.43[b]

Note: SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; EC, electrical conductivity. Different lowercase letters within the same column indicate significant (P<0.05) differences among different elevations or years. Mean±SE.